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## Illegal Hunting on the Masoala Peninsula of Madagascar: Its Extent, Causes, and Impact on Lemurs and Humans

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**ILLEGAL HUNTING ON THE MASOALA PENINSULA OF MADAGASCAR: ITS EXTENT, CAUSES,  
AND IMPACT ON LEMURS AND HUMANS**

A Dissertation Presented

by

CORTNI BORGERSON

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment  
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2015

Anthropology

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## **ABSTRACT**

### **ILLEGAL HUNTING ON THE MASOALA PENINSULA OF MADAGASCAR: ITS EXTENT, CAUSES, AND IMPACT ON LEMURS AND HUMANS**

May 2015

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Two of the greatest challenges we face in the world today are: (1) reducing human poverty and malnutrition; and (2) slowing the loss of global biodiversity. Madagascar ranks nearly last in global food security, and is one of the most biodiverse countries in the world. Within Madagascar, the Masoala Peninsula is one of our greatest conservation priorities. I use one year (July 2011 – June 2012) of lemur surveys, habitat sampling, direct observations of forest mammal hunting, eleven months of daily 24-hour recall surveys, and interviews of all households in one focal village on the Masoala peninsula of Madagascar to examine the extent of illegal hunting, its causes, and its impact on endangered lemurs and humans. I found that members of 97% of households ate forest mammals in the prior year and 26% of men intentionally trapped lemurs. While this hunting had a greater impact than habitat loss on *Eulemur albifrons*, habitat loss had a greater impact than trapping on *Varecia rubra*. There was strong seasonal variation in hunting; lemurs and bushpigs were predominately targeted

during the cool, wet austral winter, and carnivorans were targeted during the warm austral summer because of seasonal variation in prey characteristics. Forest animals were caught largely for individual consumption, and were not intended for sale or economic gain. Poverty and health most accurately predicted a man's decision to engage in illegal lemur trapping. Notably, neither working in ecotourism nor knowledge of hunting laws had an impact on the decision to trap lemurs. These findings support growing evidence that the key to successful lemur conservation may be improving rural human health and welfare. By modeling this dynamic human, lemur, and forest system, I also simulated the futures of lemurs, human, and their shared habitats under different conservation scenarios. This dissertation exemplifies a growing trend in conservation research: rather than focusing strictly on the ecological needs of endangered primate species, researchers are studying the interactions of primates and humans in shared habitat spaces.

Keywords: Madagascar, Masoala, conservation, health, system dynamics modeling, hunting, bushmeat, threats, lemurs, euplerids, carnivorans, tenrecs, bushpigs, *Varecia rubra*, *Eulemur albifrons*



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## CHAPTER 1

### INTRODUCTION

Two of the greatest challenges we face in the world today are: (1) reducing human poverty and malnutrition; and (2) slowing the loss of global biodiversity. Madagascar ranks nearly last in global food security (EIU 2014), and is one of the most biodiverse countries in the world (Myers et al. 2000). Within Madagascar, the Masoala Peninsula is one of our greatest conservation priorities (Kremen et al. 1998, Kremen et al. 2008). The Masoala National Park protects 240,520 hectares of forest and marine habitat and over 50% of Madagascar's species-level biodiversity. These same forests also provide valuable economic and health benefits to the area's 85,000 rural residents (Holmes 2007). Unfortunately, this region has been at the center of the recent (and continuing) rosewood crisis and recent surges in corruption (Waeber and Wilmé 2013). Habitat loss is accelerating (Allnutt et al. 2014) and numerous endangered species are illegally eaten there, including the white fronted brown lemur (*Eulemur albifrons*), the elusive fosa (*Cryptoprocta ferox*), and two species of sea turtle (*Chelonia mydas* and *Eretmochelys imbricata*) (Chapter 3). This dissertation examines why people choose to illegally hunt endangered species on the Masoala Peninsula and the impact this has on humans, endangered species, and the environment.

Conservationists and public health officials face serious challenges in implementing their action plans on the Masoala Peninsula (Chapter 5). I seek to increase the attainability of conservation goals by providing rigorous data on the extent

of hunting on the Masoala Peninsula, and its impact on lemurs and humans.

Specifically, I answer the following four questions:

**(1) Should we even focus our conservation efforts on hunting?**

Threats to primates result from the complex relationship between ecological processes and the direct and the indirect impacts of humans. Yet we know little about the proportional impacts of hunting and changes to habitat on individual primate species. This knowledge is critical to effective conservation. In chapter two, “The effects of illegal hunting and habitat on two sympatric endangered lemurs,” I use primate surveys, habitat analysis, interviews, and one year of direct observation of hunter behavior and catch to compare the relative impacts of altered habitat and snare trapping on two sympatric lemur species: the two largest-bodied and most endangered lemurs on the Masoala peninsula of Madagascar, *Varecia rubra* (the red ruffed lemur; Critically Endangered) and *Eulemur albifrons* (the white-fronted brown lemur; Endangered).

**(2) When do people hunt lemurs, and how can knowing this help us to optimize conservation efforts?**

Understanding seasonal hunting patterns can increase the efficacy of conservation and public health action by providing detailed information on the timing of threatened species hunting and on the incentives that drive within-year variation in human behavior. Since energy and funds available to implement policies are limited,



focusing such efforts in the most critical times of year would make best use of limited time and money. In chapter three, "Optimizing conservation policy: the importance of seasonal variation in hunting and meat consumption on the Masoala Peninsula of Madagascar," I use one year (July 2011 – June 2012) of direct observations of forest mammal hunting, eleven months of daily 24-hour recall surveys, and interviews of all households in one focal village on the Masoala peninsula of Madagascar to examine the seasonal variation in the consumption of animal-based foods and the impact this variation has on wildlife and people.

### **(3) Who hunts lemurs and why?**

Conservation policies often assume that people will stop or decrease illegal hunting if they are less poor, have greater access to affordable meat from domesticated animals, are better educated, are healthier, are involved in ecotourism, or have greater knowledge of laws prohibiting or regulating the hunting of wild animals. These assumptions may or may not be correct, and, surprisingly, are often not well tested where conservation policies are implemented. Furthermore, we often cannot reliably predict who is most likely to engage in illegal hunting. This makes it difficult to identify those people who might benefit from positive action, and ensure they are included in conservation efforts. In chapter four, "Who hunts lemurs and why they hunt them," I asked every one of a focal village's households over 600 questions about their daily resource use, socioeconomics, health, and micro- and macro- sociopolitical resource regulation to answer the questions: (1) Why do people hunt threatened lemurs, so that

we may design conservation policies that address the incentives of lemur-hunters, and;

(2) How do we identify households that are at high risk of hunting lemurs, so that we may increase the chance that combined human-livelihood and conservation efforts actually reach hunters?

**(4) How do the dynamic interactions of lemurs, habitat, and humans, impact their respective futures? How can we use this information to improve the efficacy of conservation and to design conservation strategies that are mutually beneficial for wildlife and human health and welfare?**

Untangling coupled human-environmental systems is essential to effective conservation. In chapter five, "A system dynamics approach to endangered lemur conservation on the Masoala Peninsula of Madagascar," I build a systems dynamics model using STELLA to evaluate the complex interactions among humans, two species of endangered lemur (*Varecia rubra* and *Eulemur albifrons*), and habitat. Using this model I: (1) estimate *Varecia rubra* and *Eulemur albifrons* population viability at the study site; (2) identify the social variables most critical in influencing local lemur population viability; (3) evaluate sustainability and future trends in lemur population viability under alternative hunting and behavioral scenarios; (4) begin to examine the challenges conservationists will face in the region by simulating the efficacy and consequences of potential conservation strategies; and (5) identify gaps in our knowledge and suggest future avenues of policy-relevant research.

**CHAPTER 2**

**THE EFFECTS OF ILLEGAL HUNTING AND HABITAT ON TWO SYMPATRIC ENDANGERED**

**LEMURS**

**Abstract**

Threats to primates result from the complex relationship between ecological processes and the direct and the indirect impacts of humans. Yet we know little about the proportional impacts of hunting and changes to habitat on individual primate species. This knowledge is critical to effective conservation. I used primate surveys, habitat analysis, interviews, and one year of direct observation of hunter behavior and catch to compare the relative impacts of altered habitat and snare trapping on two sympatric lemur species: the two largest-bodied and most endangered lemurs on the Masoala peninsula of Madagascar, *Varecia rubra* (the red ruffed lemur; Critically Endangered) and *Eulemur albifrons* (the white-fronted brown lemur; Endangered). Results indicate that alteration of habitat and hunting shape local faunal communities in species-specific ways. While alteration of habitat had a greater effect than snare trapping on the populations of *V. rubra*, snare trapping had a greater effect than habitat on the populations of *E. albifrons*. Therefore conservation action plans for *V. rubra* and *E. albifrons* may benefit from individual tailoring. These findings illustrate the need to consider the different manners in which habitat change and hunting affect sympatric primate species when designing conservation policy.

## **Introduction**

As humans hunt threatened species for food and alter the species' habitats to better suit the needs of people, primates are increasingly vulnerable to local extirpation and extinction (Cowlshaw and Dunbar 2000, Oates 2013). We know much about the effects of habitat alteration (Marsh 2003) and hunting (Fa et al. 2002, Fa et al. 2006, Milner- Gulland et al. 2003) on threatened primate species. We know relatively little, however, about the proportional effects of habitat alteration vs. illegal hunting on primates (de Thoisy et al. 2005, Oates 1996, Rovero et al. 2012). Understanding how individual primate species respond to multiple threats and how these responses vary among species will greatly inform assessments of extinction risk and the conservation efforts aimed at mediating this risk.

Whereas direct human impacts such as hunting likely played a major role in the extinction of primates in the past, habitat alteration may be more important in the present (Godfrey and Irwin 2007). There are numerous ways to alter a habitat, and these can affect extant primate species differently. Canopy-dwelling primates can be most affected by the loss of canopy that results from change in habitat due to expanding agriculture (Isaac and Cowlshaw 2004). Highly specialized primates can be most affected by change in habitat resulting from human forestry (Isaac and Cowlshaw 2004). Frugivorous primates that depend on patchily distributed resources can also be more sensitive to changes in habitat due to human activity than would folivorous primates (Johns and Skorupa 1987). Indeed, the composition of an extant primate's diet can be the best predictor of its risk of local extirpation (Godfrey and Irwin 2007).

In contrast, hunting can have a greater impact on primate species with the traits preferred by hunters, including those with the highest return per unit of effort invested in hunting (Fa et al. 2002; Godfrey and Irwin 2007). Body size often correlates with pressure from hunting; this relationship may stem from the potential for a higher return per unit of investment in hunting a large-bodied species (Isaac and Cowlshaw 2004; Jerozolinski and Peres 2003). However, multiple factors interact to determine a species' perceived value or profitability, including how easy it is to catch (Fa et al. 2005), and its ease of transport, taste (Schenck et al. 2006), and rarity (Courchamp et al. 2006). Frugivorous species can be predictably found at fruiting trees, which may increase their vulnerability to hunters and reduce the time that hunters spend locating prey (Hill and Padwe 2000). Canopy-dwelling species have also been found to be more vulnerable to hunting, perhaps because they are easier to locate as they loudly and conspicuously move through the canopy (Rovero et al. 2012). Hunters may also choose not to pursue particular prey that would otherwise be valuable because of various cultural and institutional prohibitions (Jones et al. 2008; Kümpel et al. 2008; Lingard et al. 2003).

Hunting can be targeted, opportunistic, incidental (in the form of less valuable by-catch), or accidental (valueless by-catch), and each method can contribute to the depletion and eventual extinction of species (Branch et al. 2013). Different methods of targeted hunting, i.e., pursuit hunting vs. snare trapping, are likely to affect individual species differently (Rowcliffe et al. 2003). It is important to know which methods are

being used to hunt extant primates and consider the different effects each of these methods may have on hunted species.

We know especially little about the proportional effects of habitat alteration vs. illegal hunting in Madagascar, one of the world's most ecologically diverse places and the location of many endemic threatened species. Ninety percent of Madagascar's lemurs are threatened with extinction (Schwitzer et al. 2013). Recent research has significantly expanded our understanding of hunting in Madagascar. The subsistence consumption of forest mammals is widespread (Gardner and Davies 2014, Golden 2009, Golden et al. 2011, 2013, 2014, Jenkins and Racey 2008, Jenkins et al. 2011, Randrianandrianina et al. 2010, Razafimanahaka et al. 2013). This wild-caught meat provides significant nonmarket economic and nutritional benefit to local people (Golden et al. 2011, 2014). Whereas a wide variety of hunting methods are used, lemurs appear to be caught predominantly by means of passive snare traps (Golden 2009). Lemurs are strictly protected in Madagascar, and lemur hunting is prohibited by national law (Decree No. 2006-400). Many lemur species may, nevertheless, be hunted unsustainably (Golden 2009).

This paper compares the relative impacts of habitat alteration and illegal snare trapping on two sympatric lemur species: the two largest and most endangered lemurs on the Masoala Peninsula of Madagascar, *Varecia rubra* (the red ruffed lemur; Critically Endangered; endemic) and *Eulemur albifrons* (the white-fronted brown lemur; Endangered) (Schwitzer et al. 2013). Specifically, to analyze the relative effects of alteration of habitat (either from humans or natural events) and trapping on these two

threatened species, I: 1) assess the density and abundance of these two lemurs at two forest sites that capture differences in human habitation and protection status; 2) document the variation in forest structure and plant characteristics at the two study sites; 3) measure the intensity of *V. rubra* and *E. albifrons* trapping and consumption at each site; and 4) examine how hunting and habitat affect *V. rubra* and *E. albifrons*.

Prior studies of *Varecia rubra* and *Eulemur albifrons* might suggest that changes in habitat would have a greater effect on populations of *V. rubra* (Vasey 2000). Prior studies of hunting in nearby Makira Natural Park have also shown that *E. albifrons* is heavily hunted (Golden 2009). *V. rubra* and *E. albifrons* differ in their size (3.5 vs. 2 kg), conspicuousness (bright red in color vs. predominately brown), activity cycles (diurnal vs. cathemeral), and vocal behavior (loud vs. more cryptic) (Mittermeier et al. 2010; Vasey 2000, 2003). Although these characteristics are likely to increase *V. rubra*'s vulnerability to pursuit hunting, they are unlikely to increase the species' vulnerability to snare hunting. *V. rubra* also have very narrow habitat and dietary niche dimensions when compared to *E. albifrons* (Vasey 2000, 2002). *V. rubra* are highly frugivorous; 88% of their diet is composed of fruit (vs. 69% in *E. albifrons*). *V. rubra* depend on the largest trees (tall, large crowns, and large diameter at breast height [DBH]). They spend 94% of their time in tree crowns, and more than 74—85% of their time in trees with a DBH of 41—80 cm, whereas *E. albifrons* are more flexible in their use of the forest and range primarily <15 m (Rigamonti 1993; Vasey 2000, 2002). This suggests that although *V. rubra* may inhabit the village site, they may do so at lower densities than *E. albifrons*. Further, the ecological flexibility, potentially higher densities, and lower

ranging behavior of *E. albifrons* may also increase the catch per unit of effort of this, albeit smaller, species. Therefore, I predict that: 1) habitat will have a greater impact than snare trapping on *V. rubra*, and 2) snare trapping will have a greater impact than habitat on *E. albifrons*.

## **Methods**

### **Study Area**

Masoala National Park (Figure 1), a UNESCO World heritage site, is one of Madagascar's largest, most remote, and most biodiverse protected areas (Kremen 2003). Ten species of lemurs are found on the peninsula (*Varecia rubra*, *Eulemur albifrons*, *Haplemur griseus*, *Microcebus rufus*, *Allocebus trichotis*, *Cheirogaleus medius*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, and *Daubentonia madagascariensis*).

Deforestation and other modifications of habitat on the Masoala Peninsula are due primarily to subsistence agriculture but also include the subsistence collection of timber and non-timber forest products and the illegal commercial collection of hardwoods species and illegal mining for quartz (Holmes 2007). Although local people are farmers rather than hunter-gatherers, they do hunt lemurs and other local species on the peninsula (Golden et al. 2014), and hunted species play an important role in the local subsistence economy (Golden et al. 2014) and in human health (Golden et al. 2014).



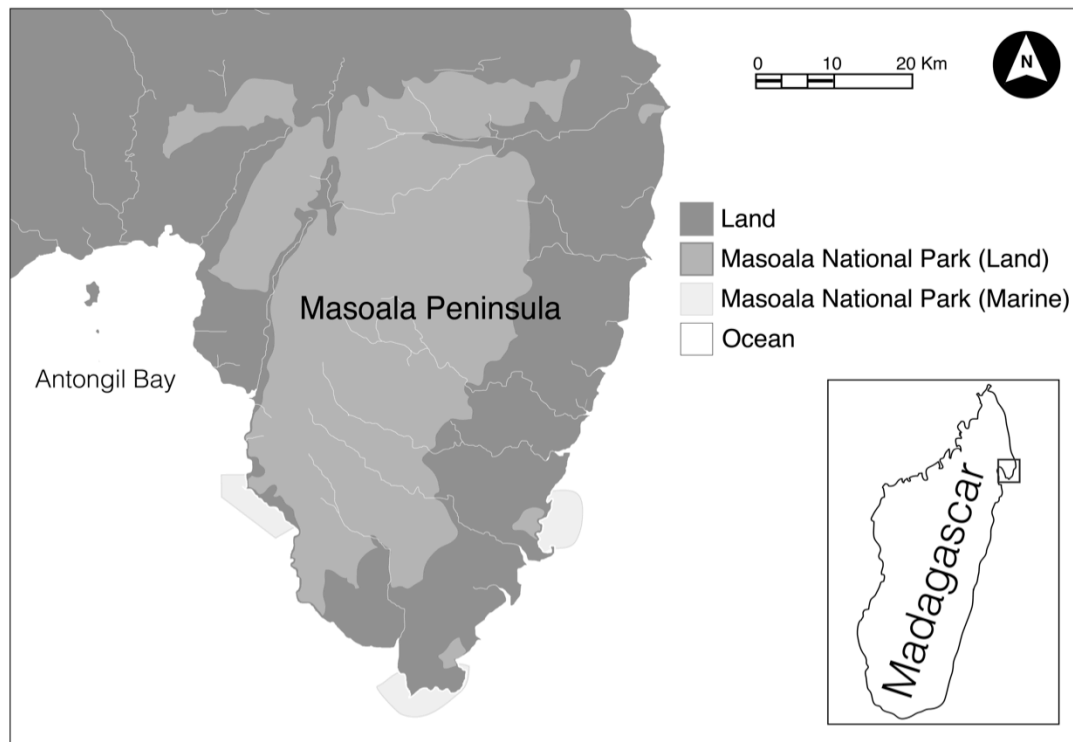


Figure 1. Study region. The precise locations of the two sites on the Masoala Peninsula (2011-2012) are not shown to protect the anonymity of the village.

I conducted this study over 12 consecutive months at two forest sites on the Masoala Peninsula. The first site, hereafter referred to as the village site, contains a small coastal village (population of 118) and forest both within and outside of Masoala National Park. The second site, hereafter referred to as the site without a village, is entirely within Masoala National Park (Figure 2) and has never contained a village. The site without a village has been protected within Masoala National Park since 1997 (Kremen et al. 1999). The national park's office has appointed a guardian at the coastal border of this site; one of the guardian's responsibilities is to prevent local people from entering the protected area. Both sites are coastal rain forests; the forests are lowland but mountainous, and unfragmented. They are also connected to each other

via Masoala National Park and are >25 aerial miles from the nearest road. I selected the site without a village because this protected site is believed to have experienced the least human disturbance of all coastal forests on the Masoala Peninsula (Masoala National Park staff, pers. comm.). Rapid assessments of resource use were completed in all known villages on the eastern boarder of Masoala National Park (N = 36). I selected the village site because of its similarity in habitat to the site without a village, its proximity to Masoala National Park, and the strong trust relationship that I established with village residents during my previous research in the region.

### **Data Collection**

Field assistants and I used three methods to collect data: 1) lemur surveys, 2) habitat sampling, and 3) focal-hunter shadowing and extensive interviews. Four field assistants helped with the collection of data for the lemur surveys and habitat sampling. The dedicated Malagasy field assistants are residents of the study village and participated in the interviews of household resource use. The identities of these assistants are being kept anonymous, at their request, for the sake of their own safety, and for the safety of the hunter and other residents of the village who cooperated with the study.

### **Lemur Surveys**

We surveyed lemurs using distance sampling methods (Buckland et al. 1993, Buckland 2001) to assess the density and population characteristics of *Varecia rubra* and *Eulemur albifrons* at both sites. I chose to survey *V. rubra* and *E. albifrons* because density can be determined more reliably for these lemurs using line transect survey

methods than for any other lemur species on the peninsula. We established ten 500 m (range = 459 – 983 m, mean = 620.85 m) triangular transects in two rows of five, extending inland from the coast, for a total of 20 transects (Figure 2). The transects varied slightly in size and shape because of restrictions created by habitat and terrain. We walked the transects one or two times monthly at a maximum rate of 1 km/h, over 12 months. Each time we saw a lemur, we noted the age class, sex, and height above ground (m) of the individual. We also recorded the size of the group of lemurs (hereafter referred to as cluster size) and the age class and sex of all individuals in this group. We used a global positioning system (GPS) unit to identify, measure, and record the perpendicular distance (m) of the lemur (or the center of the lemur cluster) from the transect line.

### **Habitat Sampling**

We conducted ecological studies of the forest environment at each study site to determine how habitat affects *Varecia rubra* and *Eulemur albifrons*. We collected botanical information using forest plots (IFRI 2008). The same 20 transects used for primate surveys served for habitat sampling. We established one forest plot near each of the three points at the corners of each triangular transect, for a total of 60 plots. However, we located the center of each plot not at the point but 20 m from the transect line so our measurements of habitat would remain unaffected by the activity of surveying primates within the transect. Each of the 60 forest plots contained three concentric circles (Fig. 2). In the smallest circle (1 m radius), we sampled all small plants (plants with a DBH of <2.5 cm). We counted the number of each species of small plant and estimated the percentage of area covered by each species of

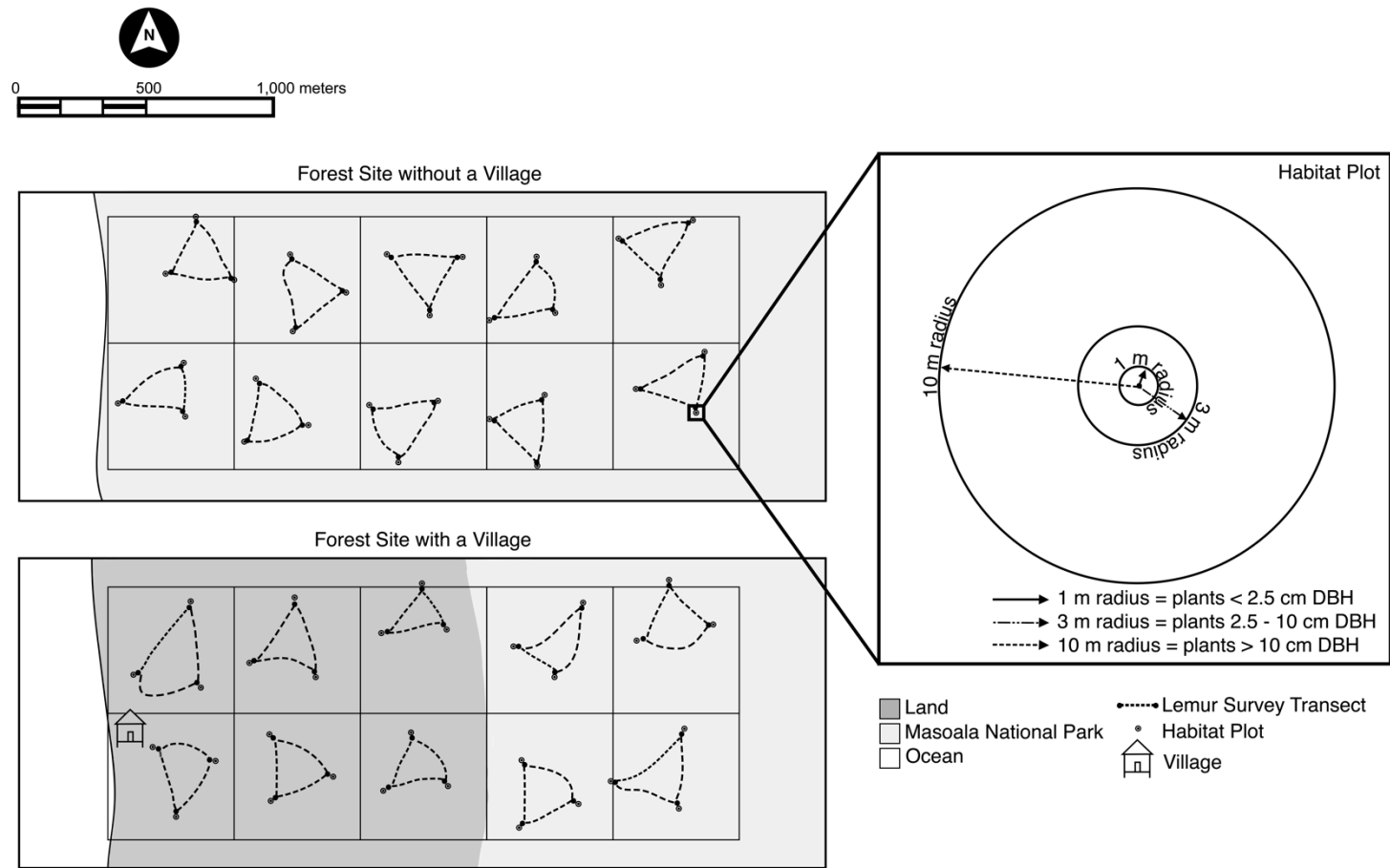


Figure 2. Study sites, lemur transects, and habitat plots on the Masoala Peninsula from 2011 to 2012.

ground cover. In the second circle (3 m radius) we identified all medium-sized plants (plants with a DBH between 2.5 and 10 cm) and measured their height and DBH. Finally in the largest circle (10 m radius), we identified all large sized plants (plants with a DBH  $\geq 10$  cm). We measured the DBH, height, crown width, crown height of all large plants, as well as percentage of land cover with evidence of human disturbance (e.g., tree cutting, machete marks, agricultural production, paths) and cyclone disturbance (e.g., land-slides, broken trees) within this largest circle. We recorded the local names of all plant species within the forest plot and whether local people said that *V. rubra* or *E. albifrons* ate those plants.

### **Hunter Shadowing and Extensive Interviews**

I speak the local dialect of Betsimisaraka and used both direct (hunter shadowing) and indirect methods (annual recall interviews and 24-hour recall surveys) to determine the intensity of the snare trapping of *Varecia rubra* and *Eulemur albifrons*.

### **Hunter Shadowing**

I recorded 12 months of direct full-day observations of the intensity and methods of lemur hunting. I followed one focal hunter over 12 months (July 2011— June 2012) during all hunting and trapping activities for two weeks per month. I collected daily self-report data from the same hunter for the entire month. I followed a single focal hunter in the village site over the entire period to assess seasonal variation in activity. Four people identified themselves as bushpig (*Potamochoerus larvatus*) hunters prior to the start of the study. Three of these hunters agreed to be shadowed by me over one year. No hunter agreed to be shadowed by a Malagasy assistant. I selected one of these

hunters, randomly, to serve as the focal hunter for the study. I obtained informed consent and the hunter fully knew about the aims and objectives of the research, as well as the possible implications of the project. I cannot and do not expect the behavior of the hunter to be representative of all hunters' behaviors. Using a single focal hunter instead offered me the opportunity to examine continuous resource use at a fine scale and to compare behavior reported in interviews and 24-hour recall surveys with the intensively observed behavior of one individual.

I recorded the following data for each hunter follow: 1) the species, age class (subadult or adult), and sex (male or female) of all captured individuals; 2) the trap size, type, and location of traps; 3) the number of snares checked, number of individuals captured (recoverable and unrecoverable), number of escaped individuals (evident from limbs left behind at the trap site, fur stuck in traps, and damage to traps); and 4) the intended destination of meat (consumption or sale and why), and expected and actual sale price. I also asked the focal hunter about the location and type of all known *laly* (each cleared area with several lemur traps is locally known as a *laly*) in the region and provided the focal hunter with a GPS to map *laly* locations.

### **Extensive Interviews**

I completed semistructured interviews, in the native dialect of Betsimisaraka, of at least one member of every household (N = 34) in the village. I do not expect the study village to be representative of general village behavior on the Masoala, but it does provide an opportunity to examine the use of lemurs by a single village in detail. I defined households as units comprising all people who shared the use of a

single kitchen. I selected participants from each household based on their availability and therefore included both men and women. I obtained informed consent from all participants. I asked participants about current household behavior, including the frequency of extraction and/or consumption of forest animal species over the last year, quantity of species harvested, and harvesting methods.

A local assistant also completed 24-hour recall surveys of one person from each household every day for two weeks per month over 11 months (August 2011—June 2012). The identities of the participants in the 24-hour recall surveys were kept anonymous to me, but participants were selected based on their availability and therefore include both men and women. Participants were interviewed about the type, quantity, and cost of all food eaten as meals and as snacks in the past 24 hours.

### **Data Analysis**

I used the software Distance (Thomas et al. 2010) to calculate densities of *Varecia rubra* and *Eulemur albifrons* from the data collected during line transect surveys. This method assumes that all lemurs located on the transect line are detected, but that the probability of detection decreases as the perpendicular distance from the transect line increases (Buckland et al. 1993, Buckland 2001). Distance calculates the detection function ( $g$ ), which corrects for the probability that a lemur will be seen at a given distance from the transect line. Distance uses this, the number of members of a species sighted ( $N$ ), the perpendicular distance of the sighted individual from the transect line ( $x$ ), and the length of the transect line ( $L$ ) to estimate the density of that species. I calculated three different probability functions (half-normal, uniform, and hazard rate),

each of which is a mathematical model of how the probability of detection might change as the distance from the observer increases. I selected the half-normal detection function based on its having the lowest Akaike's information criterion (AIC) value. I truncated no raw observations from this analysis.

I calculated the density, number, and richness (number of plant species) of each plant size class in each of the 60 forest plots, each of the 20 triangular transects, and the two sites overall. I also calculated the Shannon—Wiener diversity indices (SWDIs) and the total basal area (TBA) of medium and large plants per square hectare.

I used bivariate regression analysis to test the proportional impact of habitat (plant number, height, crown size, DBH, basal area, richness, and diversity) and hunting (the number of laly) on sightings of *Varecia rubra* and *Eulemur albifrons*. I used t-tests, analysis of variance, and  $\chi^2$  to test the differences in habitat, the impact of humans and natural events such as cyclones, hunting, and abundance of *V. rubra* and *E. albifrons* between and among: 1) the village site and the site without a village; 2) land protected within the Masoala National Park and unprotected land outside of the park; and 3) land in the village site that is protected within the park, land that is in the village site that is not protected within the park, and land in the site without a village that is protected within the park. Finally, I employed principal component analysis (with Varimax rotation) to explore further the collinearity of hunting, habitat, and the abundance of *V. rubra* and *E. albifrons*. Both habitat and lemur variables were normally distributed. Data transformations were not necessary.



## **Results**

### **Lemur Surveys**

The village site had lower densities of both *Varecia rubra* and *Eulemur albifrons* than the site without a village (Table 1). The *E. albifrons* adult male-to-female ratio did not differ between sites. This ratio was not known for *V. rubra*, which is sexually monomorphic. Both *E. albifrons* and *V. rubra* had greater subadult-to-adult ratios (2.60—4.18 times greater) and slightly larger cluster sizes (1.19—1.44 larger) at the site without a village (Table 1). We observed significantly fewer *V. rubra* and *E. albifrons* in transects where *laly* had been built within the past 15 years than in transects where *laly* had not been built (Table 2).

### **Habitat Sampling**

Large plants had significantly smaller DBH and crown size at the village site than at the site without a village (Table 3). There were also significantly more small plants at the village site. The remaining plant variables showed no statistical difference between sites (Table 3). Caution in interpreting the results of plant species richness and diversity is warranted, however, because we determined the identity of species only morphologically.

The village site had significantly more evidence of recent human disturbance than the site without a village (Table 3). Increased human disturbance in plots resulted in significantly fewer medium and large plants, and in large plants with significantly smaller height, crown size, and basal area (Table 4). In contrast, habitat disturbance

Table 1. Density and composition of *Varecia rubra* and *Eulemur albifrons* populations at two study sites on the Masoala Peninsula 2011-2012.

Variable	Site without a Village	Village Site
<b><i>Varecia rubra</i></b>		
Density (per square kilometer) (with 95% CI)	16.58 (8.07-34.05)	6.17 (2.2-13.81)
Mean cluster size (with SD)	2.87 ( $\pm$ 1.57)	2 ( $\pm$ 0.82)
Observations (Total)	85	41
Adults	70	39
Subadults and Infants	15	2
<b><i>Eulemur albifrons</i></b>		
Density (per square kilometer) (with 95% CI)	49.84 (34.5-72)	6.5 (2.96-14.24)
Mean cluster size (with SD)	5.8 ( $\pm$ 2.99)	4.88 ( $\pm$ 2.47)
Observations (Total)	172	39
Adults	124	34
Adult females	73	20
Subadults and Infants	48	5

Table 2. Observations of *Varecia rubra* and *Eulemur albifrons* in transects with and without lemur trapping on the Masoala Peninsula 2011-2012.

Lemurs (mean observations)	Transects with <i>laly</i>	Transects without <i>laly</i>	T-tests		
			t	df	P <sup>a</sup>
<i>Varecia rubra</i> (SD)	2.67 ( $\pm$ 1.63)	8.14 ( $\pm$ 6.67)	-2.88	16	<b>&lt;0.01</b>
<i>Eulemur albifrons</i> (SD)	4.83 ( $\pm$ 3.97)	13.14 ( $\pm$ 10.61)	2.54	18	<b>0.01</b>

<sup>a</sup> P values < 0.05 are indicated in bold

Table 3. Differences in habitat and hunting between two sites on the Masoala Peninsula 2011-2012.

Variable	Site without a Village	Village Site	T-tests		
			t	df	P <sup>a</sup>
Small plants (1 m radius)					
Mean number of plants per plot (SD)	31.80 (± 23.73)	60.93 (± 61.91)	2.41	37.34	<b>0.01</b>
Mean plot richness (SD)	12.13 (± 3.81)	13.77 (± 7.34)	1.08	43.59	0.28
Shannon-Wiener Diversity Index	3.53	3.52	-	-	-
Medium plants (3 m radius)					
Plants total N	268	285	-	-	-
Mean number of plants per plot (SD)	8.90 (± 3.28)	9.47 (± 6.88)	0.41	41.55	0.69
Mean plot richness (SD)	7.77 (± 2.47)	7.23 (± 4.87)	-0.53	43.03	0.60
Mean plant DBH (SD)	4.28 (± 1.7)	4.36 (± 1.66)	0.60	544.99	0.55
Mean total basal area (m <sup>2</sup> ) per plot (SD)	38.08 (± 17.21)	41.32 (± 30.77)	0.50	45.53	0.62
Mean plant height (m) (SD)	4.87 (± 2.39)	5.10 (± 2.59)	1.04	520.48	0.30
Shannon-Wiener Diversity Index	3.83	3.75	-	-	-
Large plants (10 m radius)					
Plants total N	555	513	-	-	-
Mean number of plants per plot (SD)	18.47 (± 7.52)	17.07 (± 11.24)	-0.57	50.62	0.57
Mean plot richness (SD)	14.07 (± 4.83)	12.50 (± 8.48)	-0.88	46.02	0.38
Mean plant DBH (SD)	22.24 (± 16.17)	20.24 (± 9.54)	-2.24	1039.9	<b>0.01</b>
Mean total basal area (m <sup>2</sup> ) per plot (SD)	412.88 (± 205.58)	356.80 (± 234.02)	-0.99	57.05	0.33
Mean plant height (m <sup>2</sup> ) (SD)	12.91 (± 5.26)	12.43 (± 3.65)	-1.51	1037.0	0.13
Mean plant crown size (height x width)(m <sup>2</sup> ) (SD)	42.64 (± 47.44)	36.15 (± 31.33)	-3.09	1012.4	<b>&lt;0.01</b>
Shannon-Wiener Diversity Index	3.85	3.96	-	-	-
Transect					
Mean cyclone disturbance (%) (SD)	5.17 (± 8.83)	5.93 (± 10.44)	0.17	17.51	0.86
Mean human disturbance (%) (SD)	3.37 (± 7.49)	25.27 (± 31.55)	2.14	10.01	<b>0.03</b>
Mean number of <i>Laly</i> <sup>b</sup> (SD)	0 (± 0)	3.40 (± 3.72)	2.89	9.00	<b>&lt;0.01</b>
Total					
Richness	156	182	-	-	-
Unknown 'stems'	250	385	-	-	-

<sup>a</sup> P values < 0.05 are indicated in bold

<sup>b</sup> Number of *laly* in transect area; measured habitat plots contained no *laly*.

from cyclones had little effect on medium and large plants, but it did result in significantly fewer seedlings (Table 4).

The village site had significantly more agricultural plants (this site had all of the agricultural plants found at the two sites), while the site without a village had significantly more vines and lianas (this site had 69% of all medium and 67% of all large vines and lianas found) ( $\chi^2 = 17.95$ ,  $df = 2$ ,  $P < 0.01$ ). Although the number of large plant species that are food for lemurs did not differ between the two sites ( $\chi^2 = 2.44$ ,  $df = 1$ ,  $P = 0.12$ ), the site without a village had a greater proportion of medium-sized lemur food plants ( $\chi^2 = 10.27$ ,  $df = 1$ ,  $P < 0.01$ ). Two-thirds (61 %) of all medium-sized lemur food plants were found at the site without a village. Of these medium-sized plants, there was no difference in the type of food (fruit, flowers, or leaves) available between the two sites ( $\chi^2 = 0.96$ ,  $df = 1$ ,  $P = 0.32$ ). Whereas the number of large plants that provided food for lemurs was similar at both sites ( $\chi^2 = 2.44$ ,  $df = 2$ ,  $P = 0.12$ ), the site without a village had more large plants that produce edible flowers and leaves (77 % of all large flower and leaf food plants were found at this site) ( $\chi^2 = 13.3$ ,  $df = 2$ ,  $P < 0.01$ ).

### **Hunter Shadowing and Extensive Interviews**

#### **Hunter Catch**

Over the course of a full year of observation, the focal hunter caught one *Varecia rubra* (an adult female) and fifteen *Eulemur albifrons* (three adult males, four adult females, three subadult males, three subadult females, and two of unknown sex and

age [the latter two lemurs decomposed in the trap before they were checked]). None of the caught lemurs were sold; the hunter's immediate family or a family member's household ate all recoverable lemurs.

### **Village Consumption of Lemurs**

Responses from household interviews showed that, within the lifetime of the participants, at least one member of the great majority of households had eaten *Varecia rubra* (83%) or *Eulemur albifrons* (83%). Seventy-nine percent of households had eaten both species. However, members of roughly half of households (53%) indicated they would not eat *V. rubra* or *E. albifrons* again. Members of six households ate a total of 19 *V. rubra* during the previous year and members of eight households ate a total of 41 *E. albifrons* the previous year. Villagers ate *E. albifrons* more often than any other species of lemur, i.e., more than *Varecia rubra*, *Haplemur griseus*, *Microcebus rufus*, *Allocebus trichotis*, *Cheirogaleus medius*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, or *Daubentonia madagascariensis*. All persons who hunted *V. rubra* and *E. albifrons* did so using snare traps; no hunter engaged in pursuit hunting of lemurs.

### **Lemur Hunting Methods**

Although the focal hunter had fourteen *laly*, he or she set traps in only three *laly*. The hunter rotates his or her use of *laly* from year to year, so he or she rarely uses any single *laly* in consecutive years. The hunter stops using a particular *laly* once the productivity of that *laly* drops. At this point the *laly* goes enters a "fallow" period. The hunter selects the *laly* that he or she will reestablish the next year based on the number

of years since previous use and the number of lemurs he or she observed in that area.

Unlike the trapping areas for other forest mammals, *laly* are owned by the hunter who clears the land and can be inherited. Two hunters often share these areas during a trapping season because of their high yields and because of the work involved in reestablishing *laly* sites each year (re-clearing the plant growth).

A total of 73 *laly* exist at the village site but there are no *laly* at the site without a village. Of these *laly*, 36 were of the *dilana* style and 37 were of the *kodidy* style. *Laly dilana* are long linear “roads” of land that hunters clear of plant growth, often separating two forest fragments (equivalent to *laly lava* in the nearby Makira Natural Park [Golden 2009]). Hunters then build two “bridges” across this cleared area; the only way arboreal lemurs can travel between the two forest areas is to cross a built bridge or travel a distance of  $\geq 200$  m to go around the *laly*. Hunters then build two lemur traps on each of these bridges. *Laly kodidy* are circular areas of cleared forest that surround a small forest fragment that in turn contains a fruiting tree (equivalent to *laly totoko* in Makira [Golden 2009]). Each *laly kodidy* typically contains a total of two bridges and four lemur snares. The lemur must cross the bridges containing these traps to access the fruiting tree.

In 2011—2012 the focal hunter selected one *laly dilana* and two *laly kodidy* in which to set traps. *Laly kodidy* had restricted seasonal use because the fruit trees they contain had ripe fruit for one to three months, during the austral winter. In addition, some tree species, e.g. *Canarium*, fruit once every two years. The second *laly kodidy*

was built around a tree that fruited after the first tree was no longer in fruit, maximizing the period of time that this seasonal resource could be collected.

Thirty-five *laly* (16 *kodidy* and 19 *dilana*) were located within the region containing transects used for the lemur surveys. Only six *laly* were active at the time of the regional survey. The total number of *laly* used within the entire year is unknown. Interviewees state that *laly* use is rotated and each hunter has more *laly* than he or she uses in a single year. Because I do not know which of village's *laly* were used that year, or how many lemurs each particular *laly* caught, I could not examine the effects of lemur density on trapping effort or catch. During the study year, three transects contained lemur traps (one of which was the focal hunter's). The number of *laly* in each transect region correlated positively with degree of human disturbance in habitat plots (bivariate linear regression:  $r^2 = 0.60$ ,  $F = 27.19$ ,  $P < 0.01$ ), even though the habitat plots themselves contained no *laly*. There were no *laly* within the park boundaries at either site.

#### **The Different Effects of Habitat and Hunting on *Varecia rubra* and *Eulemur albifrons***

Together, three principal components explained 82.54% of the total variation in habitat, lemurs, and hunting (Table 5). The first component captures variation in observations of *Varecia rubra*, which correlated strongly with the number of large trees, large tree TBA, large tree height, and large tree crown size. Habitat variables within “*Varecia rubra*: Indirect impacts” all negatively correlated with recent human disturbance at these sites (Table 4). The second component captures variation in the number, basal area, and height of medium-sized plants. These variables had little

influence on either *V. rubra* or *E. albifrons*. Lastly, the third component captures a strong negative correlation between observations of *E. albifrons* and the number of lemur traps, as well as a weak negative correlation between observations of *V. rubra* and the number of traps.

Although no single plant variable had a significant impact on sightings of *Eulemur albifrons* sightings, the number of sightings of *Varecia rubra* significantly positively correlated with the number of the large trees, as well as large tree TBA, height, and crown size within transect habitat plots (Table 6). Transect crown size best predicted the variation in sightings of *V. rubra* sightings ( $r^2 = 0.49$ ,  $F = 17.03$ ,  $P < 0.01$ ). Indeed, of all plant variables only the total crown size of large plants was significantly larger within forest protected within the park, regardless of site (Table 7). There were also significantly more observations of both *Varecia rubra* and *Eulemur albifrons* within forest protected within the park, regardless of site (Table 7). Once total crown size increases at the village site inside the park's boundaries, density and observations of *V. rubra* increased. In contrast, there were significantly fewer *E. albifrons* at the village site, even once they were protected within the park (ANOVA:  $F = 8.65$ ,  $df = 2$ ,  $P < 0.01$ ).



Table 4. Bivariate linear regressions showing the effects of recent habitat disturbance (by either humans or natural events) on habitat response variables at two sites on the Masoala Peninsula 2011-2012

Habitat Disturbance by Humans (% of plot with recent evidence)			
Response Variables	$r^2$	F	P <sup>a</sup>
Small plants (N)	0.05	0.06	0.81
Medium plants (N)	-0.51	6.48	<b>0.02</b>
Medium plant total basal area (m)	-0.32	2.04	0.17
Medium plant height (m)	-0.39	3.08	0.10
Large plants (N)	-0.53	7.01	<b>0.02</b>
Large plant total basal area (m)	-0.49	-5.81	<b>0.03</b>
Large plant height (m)	-0.52	6.74	<b>0.02</b>
Large plant crown volume (m)	-0.53	6.85	<b>0.02</b>
<i>Laly</i> (N) <sup>b</sup>	0.77	27.19	<b>&lt;0.01</b>
Habitat Disturbance by Cyclones (% of plot with recent evidence)			
Response Variables	$r^2$	F	P <sup>a</sup>
Small plants (N)	0.45	4.50	<b>0.04</b>
Medium plants (N)	-0.28	1.49	0.09
Medium plant total basal area (m)	0.14	0.31	0.58
Medium plant height (m)	-0.28	1.65	0.22
Large plants (N)	0.35	2.51	0.13
Large plant total basal area (m)	0.32	1.89	0.19
Large plant height (m)	0.04	0.04	0.85
Large plant crown volume (m)	0.07	0.09	0.77
<i>Laly</i> (N) <sup>b</sup>	0.07	0.10	0.76

<sup>a</sup> P values < 0.05 are indicated in bold

<sup>b</sup> Number of *laly* in transect area; measured habitat plots contained no *laly*.

Table 5. Results of principal component analyses of lemur, habitat, and hunting variables with Varimax (orthogonal) rotation.

	Orthogonally Rotated Components <sup>a</sup>		
	1 “ <i>V. rubra</i> : Indirect impacts”	2 “Medium-sized plants”	3 “ <i>E. albifrons</i> : Direct impacts”
<i>V. rubra</i> observations (Total N)	<b>0.72</b>	-0.04	0.34
Large plants (N)	<b>0.83</b>	0.29	-0.09
Large plant total basal area (m)	<b>0.92</b>	0.06	0.08
Large plant height (m)	<b>0.92</b>	0.23	0.02
Large plant total crown size (height x width)(m <sup>2</sup> )	<b>0.94</b>	0.12	0.12
Medium plants (N)	0.09	<b>0.95</b>	0.21
Medium plant total basal area (m)	0.19	<b>0.88</b>	-0.16
Medium plant height (m)	0.13	<b>0.93</b>	0.06
<i>E. albifrons</i> observations (Total N)	0.02	-0.11	<b>0.86</b>
<i>Laly</i> (N)	-0.25	-0.43	<b>-0.69</b>
Variance explained by each component			
Eigenvalue	3.92	2.89	1.45
Percent variance explained	39.15	28.90	14.48
Cumulative percent variance explained	39.15	68.05	82.54

<sup>a</sup> Component loadings of 0.50 and higher are in bold.

Table 6. Bivariate linear regressions showing the effect of plot habitat variables on *Varecia rubra* and *Eulemur albifrons* abundance at two sites on the Masoala Peninsula 2011-2012.

<i>Varecia rubra</i>			
	$r^2$	F	P <sup>a</sup>
Small plants (N)	<0.01	0.03	0.86
Medium plants (N)	0.02	0.32	0.58
Medium plant total basal area (m)	0.03	0.46	0.50
Medium plant height (m)	0.02	0.45	0.51
Large plants (N)	0.21	4.77	<b>0.04</b>
Large plant total basal area (m)	0.38	10.8	<b>&lt;0.01</b>
Large plant height (m)	0.35	9.9	<b>&lt;0.01</b>
Large plant crown size (height x width)(m <sup>2</sup> )	0.49	17.03	<b>&lt;0.01</b>
<i>Eulemur albifrons</i>			
	$r^2$	F	P <sup>a</sup>
Small plants (N)	0.02	0.38	0.55
Medium plants (N)	<0.01	0.04	0.85
Medium plant total basal area (m)	<0.01	0.11	0.75
Medium plant height (m)	<0.01	0.08	0.78
Large plants (N)	<0.01	<0.01	0.95
Large plant total basal area (m)	<0.01	0.04	0.85
Large plant height (m)	<0.01	0.09	0.77
Large plant crown size (height x width)(m <sup>2</sup> )	<0.01	0.08	0.79

<sup>a</sup> P values < 0.05 are indicated in bold

Table 7. Differences in habitat, hunting, and lemur observations in transect regions outside of and protected within the Masoala National Park 2011-2012.

Variable	Transects protected within the Park	Transects outside of the Park	T-tests		
			t	df	P <sup>a</sup>
Small plants (1 m radius)					
Mean number of plants (SD)	36.14 (± 8.54)	45.17 (± 12.11)	1.66	7.23	0.14
Medium plants (3 m radius)					
Mean number of plants (SD)	30.21 (± 9.44)	21.33 (± 14.31)	-1.40	6.95	0.21
Mean total basal area (m <sup>2</sup> ) (SD)	128.16 (± 48.73)	97.96 (± 76.60)	-0.89	6.81	0.40
Mean plant height (m) (SD)	4.55 (± 0.75)	4.73 (± 1.82)	0.23	5.74	0.83
Large plants (10 m radius)					
Mean number of plants (SD)	43.43 (± 14.18)	35.17 (± 25.30)	-0.75	6.39	0.48
Mean total basal area (m <sup>2</sup> )	1258.51 (± 449.57)	911.84 (± 380.23)	-1.77	11.23	0.10
Mean plant height (m <sup>2</sup> ) (SD)	17.18 (± 2.43)	17.98 (± 6.42)	0.30	5.62	0.78
Mean total plant crown size (height x width)(m <sup>2</sup> ) (SD)	2481.83 (± 953.84)	1626.67 (± 544.65)	-2.53	16.09	<b>0.01</b>
Hunting					
Mean number of <i>Laly</i> <sup>b</sup> (SD)	0 (± 0)	5.67 (± 3.08)	4.51	5.00	<b>&lt;0.01</b>
Lemurs (mean observations)					
<i>Varecia rubra</i> (SD)	8.14 (± 6.67)	2.67 (± 1.63)	-2.88	16.08	<b>&lt;0.01</b>
<i>Eulemur albifrons</i> (SD)	13.14 (± 10.61)	4.83 (± 3.97)	-2.54	17.91	<b>0.01</b>

<sup>a</sup> P values < 0.05 are indicated in bold

<sup>b</sup> Number of *laly* in transect area; measured habitat plots contained no *laly*.

## Discussion

Consistent with studies of African and South American primates (Linder and Oates 2011; Peres 2000; Rovero et al. 2012), this study indicates that habitat and hunting can both shape Madagascar's faunal communities in species-specific ways. Both of my predictions were strongly supported. Whereas habitat appears to have a greater effect than snare trapping on the populations of *Varecia rubra* at the study sites, snare trapping has a greater effect than habitat on the populations of *Eulemur albifrons*.

Although both habitat and hunting impact *Varecia rubra*, habitat does so to a far greater extent. Specifically, the best predictor of the population size of *V. rubra* was the total crown volume of large trees in that area. *V. rubra* are highly frugivorous and consistently use trees with the largest DBH, greatest height, and most voluminous crowns (Rigamonti 1993; Vasey 2000, 2002). To maintain their narrow niche requirements in disturbed habitats, *Varecia* expand their range and reduce the size of their community (Balko and Underwood 2005; Vasey 2000, 2005).

In contrast, subsistence-based snare trapping had the greatest effect on the populations of *Eulemur albifrons* at the sites. *E. albifrons* are more flexible in their forest use (Vasey 2000, 2002). In fact, no plant variable significantly impacted sightings of *E. albifrons* in this study. Furthermore, *E. albifrons* was the most frequently consumed lemur at the study site, and the number of lemur traps in an area had the greatest effect on population size of *E. albifrons*.

These results illustrate the importance of considering the dynamic relationship of direct and indirect human actions and each species' life history characteristics, ecology, and behavior. They lend support to several inferences. First, frugivorous canopy-dwelling primates can be most vulnerable to human alteration of habitat (Godfrey and Irwin 2007; Isaac and Cowlishaw 2004). Second, frugivores can also be vulnerable to hunting because their foraging habits are predictable (Hill and Padwe 2000). Third, frugivorous primates can differ in the degree to which alteration of habitat and hunting will impact their numbers on the basis of the restrictiveness of their habitat requirements. Finally, large body size of hunted primates may not be the best predictor of hunting pressure if the species' sensitivity to alteration in habitat either outweighs their sensitivity to hunting pressure or principally reduces their numbers in hunting areas. At Masoala, as in Makira (Golden 2009), *Eulemur albifrons* was the most frequently consumed lemur. Because lemurs were not caught using pursuit hunting, prey choice is less likely to affect their vulnerability. This may explain why there is greater hunting pressure on *E. albifrons*, the smaller, more cryptic, and less vocal of the two species. Even though *Varecia rubra* are larger, the comparatively relaxed niche requirements of *E. albifrons* (Vasey 2000), their preference for a range at a lower level of the forest (Vasey 2000), and their higher densities may make them easier to catch using snare traps. This study's focus on snare trapping provides a perspective that differs from that drawn from previous studies on pursuit-hunting where the conspicuousness of canopy-dwelling primates' travel and social behavior impact hunting success (Rovero et al.

2012). Because frequent catch of *E. albifrons* can encourage continued trapping effort, continued incidental catch of *V. rubra* may further stress populations of *V. rubra* already reduced by alteration of their habitat. This process is called “piggy-back” extinction (Clayton et al. 1997).

Although people illegally hunt lemurs outside the park’s boundaries, they obey hunting laws within the park’s boundaries. We need to conduct further research on population dynamics of *Eulemur albifrons* in the interior of the peninsula to determine if source-sink dynamics are stable or if snare trapping surrounding the park is depleting the endangered *E. albifrons*. Unfortunately we know very little about the density of populations of *E. albifrons* or *Varecia rubra* in the peninsula’s deep interior, which is characterized by mid- elevation, humid evergreen, and cloud forests instead of the lowland coastal humid evergreen forests at the studied sites (Kremen 2003). We particularly need additional information on how human activities more broadly affect these species across the Masoala Peninsula (especially in areas of commercial use, ownership and use of firearms, and high human population density).

If further research validates the results found in this study, then conservation action plans for *Varecia rubra* and *Eulemur albifrons* may benefit from individual tailoring. Both will depend on working with local people to develop viable options that increase the sustainability of their livelihoods. *V. rubra* may benefit from a greater emphasis on reducing alteration of habitat, especially the loss of large trees with voluminous crowns. *E. albifrons* may instead benefit from a greater emphasis on increasing the sustainability of human food systems. These findings illustrate the need to

consider the different manners in which habitat change and hunting affect sympatric primate species when designing conservation policy.



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**CHAPTER 3**

**OPTIMIZING CONSERVATION POLICY: THE IMPORTANCE OF SEASONAL VARIATION IN  
HUNTING AND MEAT CONSUMPTION ON THE MASOALA PENINSULA OF  
MADAGASCAR**

**Abstract**

Studying seasonal hunting patterns can be critical for developing sound conservation and public health actions. Since funds available to implement policies are limited, focusing efforts during the most critical times of year is essential. This study (July 2011 – June 2012) uses direct observations of forest mammal hunting, daily 24-hour recall surveys, and interviews of households in one focal village on the Masoala Peninsula of Madagascar to examine: (1) what drives seasonal hunting patterns; (2) how seasonal variation in wildlife and domestic meat consumption affects native species and humans; and (3) how understanding seasonal variation can improve the efficacy of conservation and public health action plans. Strong seasonal variation in forest mammal hunting and in the consumption of fish and domesticated livestock exists on the Masoala. Hunters target bushpigs, tenrecs, and lemurs during the austral winter (March – August). People eat more native and introduced carnivorans, fish, and domesticated livestock during the austral summer (September – February). Our results suggest that seasonal changes in hunting patterns are driven by the physical and behavioral characteristics of prey rather than seasonal scarcity of alternative meat. Seasonal hunting and meat consumption on the Masoala Peninsula may amplify the negative impact of hunting on native

carnivorans and tenrecs (who are hunted during pregnancy and lactation) and the positive impact of lemur, bushpig, and tenrec consumption on human health. This study illustrates an important aspect of hunting on the Masoala: people decide *whether* or not to hunt independently of their decisions regarding *when* to hunt particular species.

### **Introduction**

Reconciling the conservation and human livelihoods aspects of hunting wildlife is crucial (Barrett et al., 2011; Milner-Gulland et al., 2003). Hunting provides substantial nutritional and economic benefits to rural people, yet when practiced at unsustainable levels it also endangers wildlife and the integrity of local ecosystems (Barrett et al., 2011; Brashares et al., 2011; Golden et al., 2011; Golden et al., 2013; Myers et al., 2013). Given the large scale of hunting worldwide (Fa et al, 2006; Milner-Gulland et al., 2003), implementing effective regulations that balance the needs of people and wildlife will be difficult.

Understanding seasonal patterns in behavior can increase the efficacy of conservation action by providing detailed information on the timing of and the incentives that drive within-year variation in behavior (Packer et al., 2005; Irvine et al., 2014). In order to change unsustainable hunting practices and improve the welfare of rural people, conservation strategies must specifically address when and why humans hunt endangered species (Milner-Gulland 2012). Since the energy and funds available to implement conservation strategies are limited (Wilson et al., 2006), focusing effort on

the most critical periods of the year would also make best use of limited time and money. Thus we have good reason to develop conservation strategies that are sensitive to these seasonal patterns or cycles. However, to-date seasonal hunting patterns are still poorly understood.

Madagascar has long been recognized as a biodiversity hotspot (Myers et al., 2000). Over 90% of Madagascar's endemic lemurs and 50% of endemic euplerid carnivorans are threatened with extinction (Schwitzer et al., 2013; IUCN, 2014); yet these and other wildlife provide direct nutritional and economic benefits to Madagascar's people (Golden et al., 2011; Golden et al., 2014). Madagascar's protected areas conserve many mammals, and outside of these areas laws specify four categories of protection, from no restrictions to complete prohibition on hunting (Decree No. 2006-400). Yet the creation of these laws does not insure that people know about them (Keane et al., 2011), and knowledge of these laws does not insure their compliance. In fact, local people often greatly resent these interventions as forcing people into poverty and depriving them of a secure food supply (Keller, 2008; Sodikoff, 2009). Therefore, despite the existence of regulations, threatened species are still widely hunted for food (Barrett & Ratsimbazafy, 2009; Garcia & Goodman, 2003; Gardner & Davies, 2014; Golden, 2009; Golden et al., 2011; Golden et al., 2013; Golden et al., 2014; Goodman, 2003; Jenkins & Racey, 2008; Jenkins et al., 2011; Randrianandrianina et al., 2010; Razafimanahaka et al., 2013).



Variation in the characteristics of local human communities may affect within-year hunting patterns due to seasonal changes in economics (Golden et al., 2014), nutritional availability and value (Goodman 2006; Golden et al., 2011; Gardner & Davies, 2014), cultural norms (Jones et al., 2008), travel, and laws that define legal hunting seasons (Decree No. 2006-400). Furthermore, variation in the characteristics of wildlife may affect within-year hunting patterns due to seasonal changes in feeding and ranging behavior (Andrianjakarivelo, 2000; Randrianandrianina et al. 2010), body fat content (Gardner & Davies, 2014), and flavor (which can be affected by diet). Seasonal patterns in hunting may also differently impact prey species if this hunting coincides with seasons of mating, pregnancy, and lactation in prey species (Jenkins et al. 2008). It may also differently impact human health and welfare if this hunting coincides with seasonal food and economic insecurity (Cripps, 2009; Harris, 2011; Golden et al., 2011; Tsujimoto et al., 2012; Golden et al., 2014).

The Masoala Peninsula is one of the world's most biodiverse places and is a conservation priority within Madagascar (Kremen et al., 1999; Kremen et al., 1998). In a focal village on this peninsula, I established the number and biomass of forest mammals that were hunted, the seasonal variation in the hunting of forest mammals and the eating of all animal foods (domestic and wild-caught), and the reasons for seasonal variation in hunting. With these data I examine: (1) what drives seasonal hunting patterns; (2) how seasonal variation in hunting and meat consumption affects native species and humans; and (3) how understanding seasonal variation can improve the efficiency and efficacy of conservation and public health action plans.

## Methods

### **Study area and human context**

The Masoala National Park is a wet, mountainous, UNESCO World heritage site that is far from roads and contains some of the last remaining lowland coastal rainforest in Madagascar (Kremen et al., 1998). There are two primary seasons on the Masoala Peninsula, the wet cool austral winter (March – August) and the hot ‘dry’ austral summer (September – February). The Masoala National Park is home to ten species of lemurs (*Varecia rubra*, *Eulemur albifrons*, *Haplemur griseus*, *Microcebus rufus*, *Allocebus trichotis*, *Cheirogaleus medius*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, and *Daubentonia madagascariensis*), six euplerids (*Cryptoprocta ferox*, *Eupleres goudotii*, *Fossa fossana*, *Salanoia concolor*, *Galidictis fasciata*, and *Galidia elegans*), one introduced viverrid (*Viverricula indica*), at least four tenrecs (*Tenrec ecaudatus*, *Setifer setosus*, *Hemicentetes semispinosus*, and *Oryzorictes hova*), at least three bat species (*Pteropus rufus*, *Rousettus madagascariensis*, and *Miniopterus manavi*), introduced bushpigs (*Potamochoerus larvatus*), and numerous native and introduced rodents (Table 8) (Sterling & Rakotoarison, 1998; Garbutt, 2007; Goodman, 2012; Farris et al., 2012). Forty-eight percent of these species are threatened with extinction (IUCN, 2014; Schwitzer et al., 2013).

The area surrounding the Masoala National Park has 250 permanent villages with a total population of more than 85,000 people (Holmes, 2007). Local people are predominantly Betsimisaraka. Eighty percent make their living as agriculturalists, primarily for subsistence. The staple crop is rice; lowland irrigated rice fields are harvested during the austral summer (in December) and hillside rain fed rice fields are harvested during the austral winter (in May). Rice production is supplemented by multiple species of tubers primarily harvested in June, July, and November (AGEVAREN, 2009). In addition to agricultural activities, the local people fish, raise domesticated livestock (cows, pigs, chickens, geese, and ducks), and supplement their diet with forest animals (Golden et al. 2014).

I conducted this study over twelve consecutive months in a focal village on the Masoala Peninsula of Northeastern Madagascar. The village is small (population of 118), located on the coast, and is less than 2 km from the Masoala National Park. There is no formal market within the village.

### **Data collection and analysis**

I used both direct (focal hunter shadowing) and indirect (annual interviews and 24 hour recall surveys) methods to provide a more holistic understanding of seasonal hunting and meat consumption. This approach allowed me to study the behavior of hunters and consumers at the individual, household, and village levels. By comparing the results of multiple methods I can also evaluate their strengths and weaknesses and control for the inevitable biases in how individuals recall and report behavior.

### **Focal hunter follows**

I first identified all known hunters of bushpigs within the village. Bushpigs are an introduced species and are considered a local pest. They can be legally hunted outside of the park (Decree No. 2006-400) and hunters freely discuss their trapping within the presence of other community members. Once I had identified all known bushpig trappers, I randomly selected one bushpig-trapper to serve as the focal hunter for the study. I discussed the aims, objectives, and the possible implications of the project with the hunter, and he consented to being followed. I followed the trapper two weeks per month over twelve months (July 2011 to June 2012) and collected self-report data every day each month. During each follow I collected data on the number of animals captured (recoverable and unrecoverable) and estimated the potential number of escaped animals (evident from missing limbs, fur, feathers, and damage left behind at snare traps). For each animal caught, I recorded species, age class, and sex. When possible, I also weighed and measured carnivorans, insectivores, and lemurs using a spring scale and measuring tape. Bushpigs were too large to weigh in their entirety; I weighed the cut portions of bushpig meat and used these to estimate their total weight. I also interviewed the hunter during all trapping activities about his rationale for seasonal trapping strategies.

### **Annual village interviews**

I completed 37 extensive, semi-structured interviews of at least one member of 100% of village households. I defined a 'household' as a group of people who share the

use of a single kitchen. I speak the local dialect of Betsimisaraka and completed the interviews without a Malagasy assistant. I asked members of each household if they trapped, caught, and/or ate each of 27 forest mammals (Table 8) in the prior year. For each species the interviewee had eaten, I also asked how it was captured, why it was captured (e.g. for food and/or because of human-wildlife conflicts), if the species was available or eaten seasonally, the season it was available, the season it was eaten, and any reasons for variation over time in any of these factors. Interviewees rarely referred to seasons by months, but rather referred to important seasonal indicators including crops, fruiting and flowering trees, thunder, and the names of moons.

#### **24 hour recall surveys**

A local assistant native to the study village conducted 24-hour recall surveys of diet two weeks per month over 11 months (August 2011-June 2012). The assistant will remain anonymous to protect the identity of the hunter and village. We asked one member of each household about the entire households' activities, income, expenditures, extraction, and food and drink consumed (identity, amount, source, and cost) for each meal and as snacks in the past 24 hours. My assistant kept each household's identity anonymous by not labeling households by name or number. We excluded only one household from data collection during the second half of the study because of inter-personal conflict (unrelated to this research) with the field assistant collecting the data.

## **Data analysis**

I calculated the total number of individuals and the total biomass of each forest mammal species consumed by the entire village each month using the annual interview data. I determined the total biomass by using the weights collected from hunter follows in this study (described above) and also from weights published in Goodman (2012) and Garbutt (2007).

I assessed the seasonal variation in the hunting and consumption of forest mammals using data from the focal hunter follows and the annual interviews. From these data I calculated the total number and biomass of forest mammals that were hunted and eaten each month. I then subdivided this total into the number and biomass of euplerids, viverrids, megachiroptera, microchiroptera, tenrecs, bushpigs, and lemurs eaten each month. Finally, I used a hierarchical cluster analysis with Ward's metric to test if the structure of animal species reflected seasonal hunting patterns.

I determined the seasonal variation in the consumption of all animal foods using data from the 24-hour recall surveys. I excluded the first month of data from the analysis as a sensitization period. From the remaining ten months of data I calculated mean number of meals each month that included any animal food, and then subdivided this into meals with marine or freshwater animals (hereafter summarized as 'fish,' though turtles and invertebrates were also eaten), domestic animals, and forest animals (which included both forest mammal and avian species).

To examine the potential reasons for seasonal hunting I used bivariate linear and multiple regression to test if the consumption of domestic animals or fish (calculated

from 24-hour recall surveys) could predict either the consumption of forest mammals (calculated from annual interviews) or hunter effort (focal hunter follows). I also used bivariate linear regressions to test if hunter effort was correlated with the total, recoverable, or lost amount of biomass the hunter caught each day (focal hunter follows). I compared seasonal hunting behavior (annual interviews and focal hunter follows) with laws that designate the protected status of wildlife species or hunting seasons (Table 8) (Decree No. 2006-400). I calculated the percentage of active hunters that cited seasonal variation in human factors (financial/food insecurity, cultural norms, travel, or laws) and prey characteristics (ranging behavior and body fat content) as an incentive for hunting each animal seasonally (calculated from annual interviews).

Finally, to examine the impact of hunting patterns on wildlife and people I compared seasonal hunting patterns (calculated from annual interviews and focal hunter follows) with: (1) seasonal periods of mating and offspring dependency in each forest mammal species; and (2) with seasonal periods of food insecurity from crop (AGEVAREN, 2009) and animal (calculated from 24-hour recall surveys) based foods within the village.

## **Results**

### **The extent of forest mammal hunting and consumption**

The focal hunter and other hunters within the village caught forest mammals using snare traps or caught opportunistically using sticks, machetes, dogs, or (less frequently) slingshots. The focal hunter built snare traps that targeted one or two specific species and then had a broad range of by-catch within (and occasionally outside

of) that taxon. By-catch was incidental (non-targeted animals that were of equal or lower value) but not accidental (non-targeted animals of no value). The focal hunter and other hunters within the village caught forest mammals for subsistence or because of human-wildlife conflicts (e.g. when *Cryptoprocta ferox* ate poultry within the village or *Potamochoerus larvatus* ate farmed tubers). Animals that were caught because of human-wildlife conflict were also eaten.

Villagers ate a total of 292 forest mammals and 1,148.73 kg (before processing) of forest mammal biomass over one year (Table 9). The focal hunter caught 58 of these animals and 390.54 kg of this biomass (Table 9). The two most consumed taxa in number were tenrecs (36%) and lemurs (26%); whereas the two most consumed taxa in biomass were bushpigs (65%) and lemurs (13%) (Table 10).

### **Seasonal variation in the hunting and eating of animal foods**

Villagers reported eating an average of  $1.29 \pm \text{SD } 0.19$  meals with some source of animal food (wild or domestic) each day. More meals contained animals during the austral summer (Figure 3). Of this animal food, 89% was from fish, 9% was from domestic animals, 2% was from forest animals. Fish and domestic animal consumption peaked during the summer and forest animal consumption peaked during the winter (Figure 3).



Table 8. The protected status, laws, and practiced hunting seasons of forest mammals on the Masoala Peninsula (2011-2012).

Species name	IUCN status <sup>a</sup>	National protection status <sup>b</sup>	Regulated hunting season <sup>b</sup>	Practiced hunting season <sup>c,d</sup>
<i>Eulemur albifrons</i>	EN	Strictly Protected	Prohibited	Mar – Aug
<i>Varecia rubra</i>	CR	Strictly Protected	Prohibited	Mar – Aug
<i>Microcebus rufus</i>	VU	Strictly Protected	Prohibited	All months (peaks Oct – Nov, Feb – Mar)
<i>Allocebus trichotis</i>	VU	Strictly Protected	Prohibited	All months
<i>Cheirogaleus medius</i>	LC	Strictly Protected	Prohibited	All months (peaks Mar – Aug)
<i>Phaner furcifer</i>	VU	Strictly Protected	Prohibited	Rarely hunted
<i>Lepilemur scottorum</i>	EN	Strictly Protected	Prohibited	Rarely hunted
<i>Haplemur griseus</i>	VU	Strictly Protected	Prohibited	All months (peaks Mar – Aug)
<i>Avahi mooreorum</i>	EN	Strictly Protected	Prohibited	All months
<i>Daubentonia madagascariensis</i>	EN	Strictly Protected	Prohibited	Not hunted
<i>Galidia elegans</i>	LC	Game	Apr 1 - Jun 30	All months (peaks Oct – Dec, Mar)
<i>Galidictis fasciata</i>	NT	Game	Apr 1 - Jun 30	All months (peaks Mar)
<i>Salanoia concolor</i>	VU	Game	Apr 1 - Jun 30	All months
<i>Cryptoprocta ferox</i>	VU	Protected	Restricted	Oct – Dec, Mar
<i>Fossa fossana</i>	NT	Protected	Apr 1 - Jun 30	Sep – Dec
<i>Eupleres goudotii</i>	NT	Protected	Apr 1 - Jun 30	Sep – Dec
<i>Tenrec ecaudatus</i>	LC	Game	Apr 1 - May 31	Oct – May (peaks Jan – May)
<i>Setifer setosus</i>	LC	Game	Apr 1 - May 31	Oct - Apr
<i>Hemicentetes semispinosus</i>	LC	Game	Apr 1 - May 31	All months (peaks Jan – Mar)
<i>Oryzorictes hova</i>	LC	Game	Apr 1 - May 31	Not hunted
Native forest rats		Not Listed	Unrestricted	Not hunted (for food)
Introduced rats	LC	Nuisance	Unrestricted	Not hunted (for food)
<i>Potamochoerus larvatus</i>	LC	Nuisance	Unrestricted	All months (peaks May – Aug)
<i>Pteropus rufus</i>	VU	Game	May 1 - Sep 1	All months (peaks Oct – Nov, Jan – Feb)
<i>Miniopterus manavi</i>	LC	Game	Feb 1 - May 1	All months
<i>Rousettus madagascariensis</i>	NT	Game	May 1 - Sep 1	Nov – Dec, Feb – Mar
<i>Viverricula indica</i>	LC	Nuisance	Unrestricted	Sep – Dec

<sup>a</sup> IUCN 2014, Schwitzer et al. 2013, <sup>b</sup> The protected status and legal hunting season of each species as designated by Malagasy law (Decree No 2006-400)

<sup>c</sup> The season each species is actually hunted by local people, <sup>d</sup> Data collected from household interviews and focal hunter follows

Table 9. The number of forest mammals caught, method of hunting used, and reasons for seasonal hunting in a village on the Masoala Peninsula of Madagascar (2011-2012).<sup>e</sup>

Species name	Focal hunter catch (n)	Total village catch (n)	Hunting type	Hunted seasonally? <sup>a</sup>	Incentives for seasonal hunting <sup>b</sup>					
					Seasonal variation in human characteristics				Seasonal variation in prey characteristics	
					Food/financial insecurity	Cultural norms	Laws	Travel to other towns	Ranging behavior	Body fat content
<i>Eulemur albifrons</i>	15	36	Targeted	88	0	0	0	0	71 <sup>d</sup>	29
<i>Varecia rubra</i>	1	19	Targeted & Incidental	71	0	0	0	0	71 <sup>d</sup>	29
<i>Microcebus rufus</i>	0	2	Opportunistic	50	0	0	0	0	100 <sup>c</sup>	0
<i>Allocebus trichotis</i>	0	0	Rarely hunted, Opportunistic							
<i>Cheirogaleus medius</i>	3	7	Opportunistic & Incidental	80	0	0	0	0	75 <sup>d</sup>	25
<i>Phaner furcifer</i>	0	0	Rarely hunted, Opportunistic							
<i>Lepilemur scottorum</i>	0	0	Rarely hunted, Opportunistic & Incidental							
<i>Haplemur ariseus</i>	1	10	Opportunistic & Incidental	43	0	0	0	0	100 <sup>c</sup>	0
<i>Avahi mooreorum</i>	0	1	Opportunistic & Incidental	0	0	0	0	0	0	0
<i>Daubentonius madagascariensis</i>	0	0	Not hunted							
<i>Galidia elegans</i>	2	7	Opportunistic & Targeted	0	0	0	0	0	0	0
<i>Galidictis fasciata</i>	0	5	Rarely hunted, Targeted & Incidental	100	0	0	0	0	100 <sup>c</sup>	0
<i>Salanoia concolor</i>	0	5	Opportunistic & Targeted	0	0	0	0	0	0	0
<i>Cryptoprocta ferox</i>	0	4	Targeted & Opportunistic	80	0	0	0	0	100 <sup>c</sup>	0
<i>Fossa fossana</i>	5	13	Targeted & Incidental	63	0	0	0	0	100 <sup>d</sup>	0
<i>Eupleres gaudotii</i>	0	5	Targeted & Incidental	50	0	0	0	0	100 <sup>d</sup>	0
<i>Tenrec ecaudatus</i>	19	95	Opportunistic & Incidental	90	0	0	0	0	75	25
<i>Setifer setosus</i>	0	7	Opportunistic	40	0	0	0	0	50	50
<i>Hemicentetes semispinosus</i>	0	3	Opportunistic	33	0	0	0	0	100	0
<i>Quanzarictes hova</i>	0	0	Not hunted (for food)							
Native forest rats	0	0	Not hunted (for food)							
Introduced rats	0	0	Not hunted (for food)							
<i>Potamochoerus larvatus</i>	5	12	Targeted	71	0	0	0	0	100 <sup>c</sup>	0
<i>Pteropus rufus</i>	0	32	Purchased & Targeted	71	0	0	0	50	50 <sup>d</sup>	0
<i>Miniopterus manavi</i>	0	8	Targeted	0	0	0	0	0	0	0
<i>Rousettus madagascariensis</i>	0	1	Opportunistic	100	0	0	0	0	100 <sup>d</sup>	0
<i>Viverricula indica</i>	7	20	Targeted	67	0	0	0	0	100 <sup>d</sup>	0

<sup>a</sup> Percentage of active hunters who report that the animal is hunted seasonally

<sup>b</sup> If hunted seasonally, the percentage of active hunters who mentioned this as an reason for hunting the animal seasonally

<sup>c</sup> Change in ranging behavior which increases the species overlap with humans, crops, or domesticated animals

<sup>d</sup> Change in ranging behavior that increases the predictability of the species location at key seasonal resources

<sup>e</sup> Data collected from focal household interviews, 24-hour recall surveys, and focal hunter follows

Table 10. The percentage of the total biomass and total number of forest mammals caught by the entire village and the focal hunter for each taxa (Masoala Peninsula 2011- 2012). Of all forest mammals eaten, people ate the amount of bushpig and lemur meat (human health impact), while they killed the greatest number of tenrecs and lemurs (conservation impact). Additionally, the focal hunter relied more on bushpigs and less on bats than your average villager.<sup>a</sup>

Species	Percentage of total biomass caught		Percentage of total number caught	
	Village	Focal hunter	Village	Focal hunter
Bushpigs	65%	80%	4%	9%
Lemurs	13%	9%	26%	34%
Tenrecs	7%	2%	36%	33%
Euplerids	7%	3%	13%	12%
Viverrids	6%	6%	7%	12%
Bats	2%	0%	14%	0%

<sup>a</sup> Data collected from household interviews and focal hunter follows

Table 11. Bivariate linear regressions showing the lack of effect of total animal, fish, and domestic animal consumption as well as trapper productivity on forest animal consumption and hunting in a focal village on the Masoala Peninsula (2011-2012).<sup>a</sup>

Independent variable	Dependent variable	r <sup>2</sup>	F	P <sup>b</sup>
Number of meals that contained domestic animals	Number of meals that contained forest animals	0.02	0.20	0.66
Number of meals that contained fish	Number of meals that contained forest animals	0.28	-3.44	0.10
Number of meals that contained domestic animals	Number of days spent trapping forest mammals	0.28	3.48	0.10
Number of meals that contained fish	Number of days spent trapping forest mammals	0.15	-0.64	0.24
Total kg of biomass caught by the focal hunter	Number of days spent trapping forest mammals	0.05	0.57	0.47
Kg of recoverable biomass caught by the focal hunter	Number of days spent trapping forest mammals	0.18	2.16	0.17
Kg of unrecoverable biomass caught by the focal hunter	Number of days spent trapping forest mammals	0.06	0.58	0.46

<sup>a</sup> Data collected from 24-hour recall surveys and focal hunter follows

<sup>b</sup> P-values less than 0.05 were considered significant

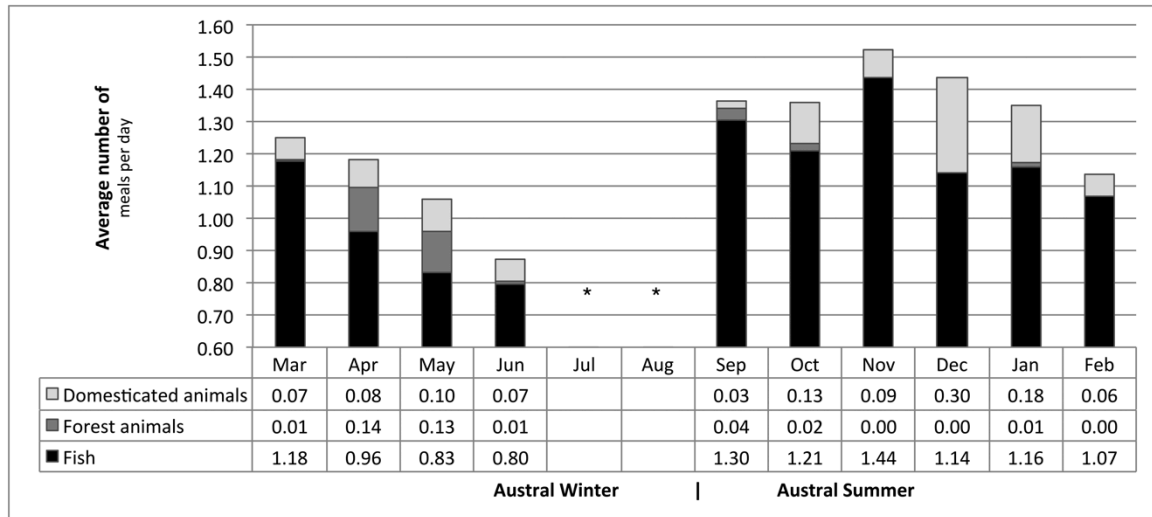


Figure 3. Seasonal variation in the consumption of animal-based foods on the Masoala Peninsula collected from 24-hour recall surveys from September 2011 until June 2012.

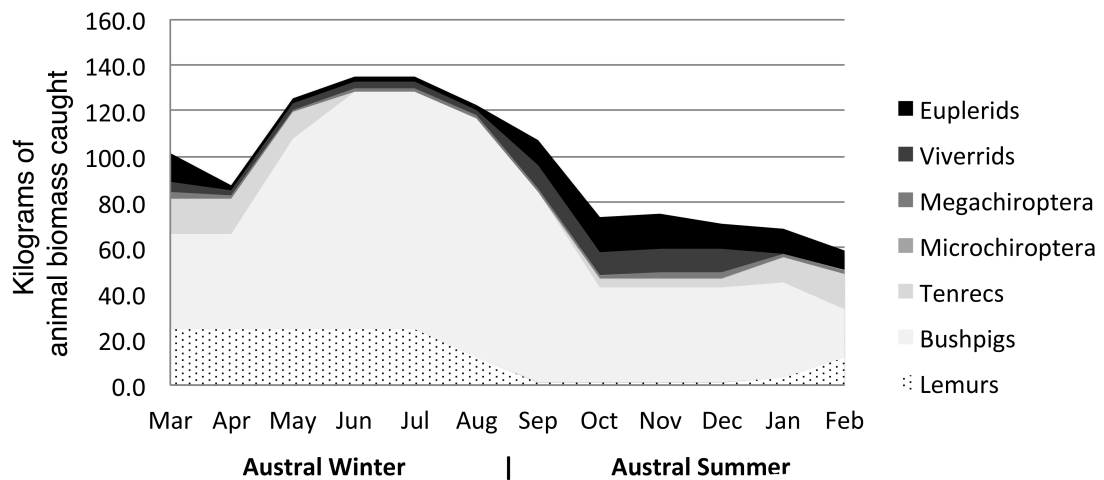


Figure 4. Seasonal changes in the biomass of forest mammals caught in a focal village on the Masoala Peninsula collected from household interviews and focal hunter follows (2011- 2012).

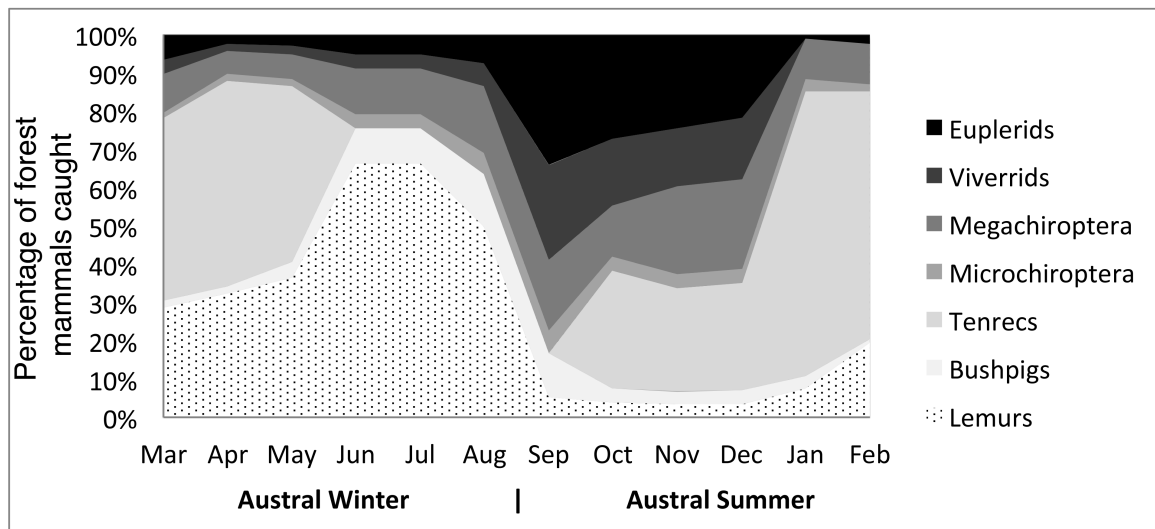


Figure 5. Seasonal changes in the percentages of individual forest mammal taxon (N) caught by members of a focal village on the Masoala Peninsula collected from household interviews and focal hunter follows (2011- 2012).

There was seasonal variation in the hunting of animal species (Table 8). People in the village increased their consumption of forest mammals during the cool, wet austral winter (Figure 4). Bushpigs, tenrecs, and endangered lemurs were predominantly eaten during this season. In contrast, native euplerid carnivorans and introduced viverrid carnivorans were eaten more during the warm austral summer (Figure 5). Data from the focal hunter follows also support these patterns in seasonal hunting. The focal hunter trapped lemurs most heavily in the austral winter, trapped small euplerids and viverrids in the austral summer, and set traps for bushpigs throughout the year. He caught more forest mammals in the early austral winter, when his catch was primarily composed of opportunistically caught tenrecs (*Tenrec ecaudatus*) and targeted lemurs

(primarily *Eulemur albifrons*) (Figure 6). While the hunter caught the most euplerids (*Fossa fossana*) and viverrids (*Viverricula indica*) in snare traps during the early austral summer, he also opportunistically caught euplerids (*Galidia elegans*) in early winter when they preyed on village poultry (Figure 6). A hierarchical cluster analysis (using Ward metrics) of the number of each forest mammal species caught by the focal trapper each month also confirmed the seasonal nature of wildlife hunting; species were clustered into three categories, those which were primarily targeted during in winter (category 1) and summer (category 3), and those which were opportunistically caught throughout the year as by-catch or from human-wildlife conflicts (category 2) (Figure 7).

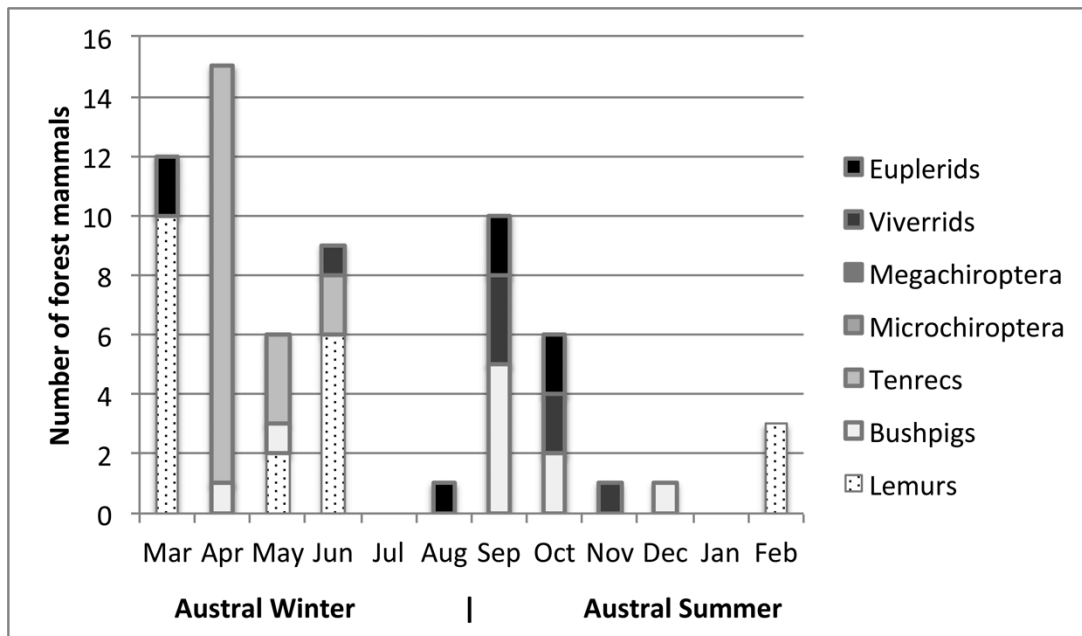


Figure 6. Seasonal variation in the number and species of forest mammals caught by a focal hunter on the Masoala Peninsula (July 2011 – June 2012).

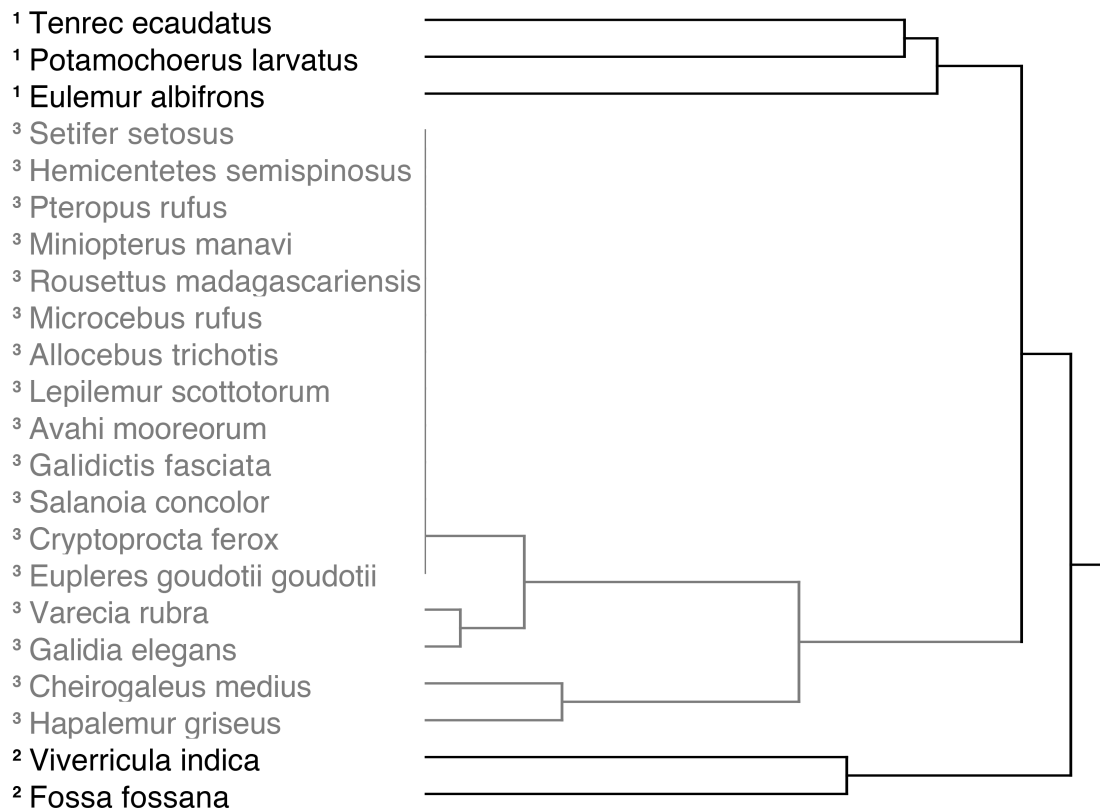


Figure 7. Hierarchical cluster analysis using the Ward metric of the number of each species caught by the focal hunter on the Masoala Peninsula each month (July 2011 – June 2012). Three clusters emerged that reflected the seasonal patterns of hunting: (1) targeted species who were trapped during the winter; (2) untargeted species that were opportunistically or incidentally caught throughout the year or because of human-wildlife conflicts; and (3) targeted species that were trapped during the summer.

Trapper effort did not significantly vary between seasons ( $T = 0.44$ ,  $DF = 9.99$ ,  $P = 0.34$ ) (Figure 8). Of the total biomass he caught over one year, 20% was unrecoverable because it either rotted in traps or was scavenged before he could collect it, 56% was eaten by members of his household, and 24% was sold (Figure 8). The hunter only sold the meat of bushpigs, which were too large for his family alone to eat. Bushpigs and lemurs provided the greatest amount of recoverable biomass per day spent trapping

from March until June, and in October (Figure 8). Unrecoverable biomass was highest from September until December (Figure 8), when animals rotted in traps because of high ambient temperatures.

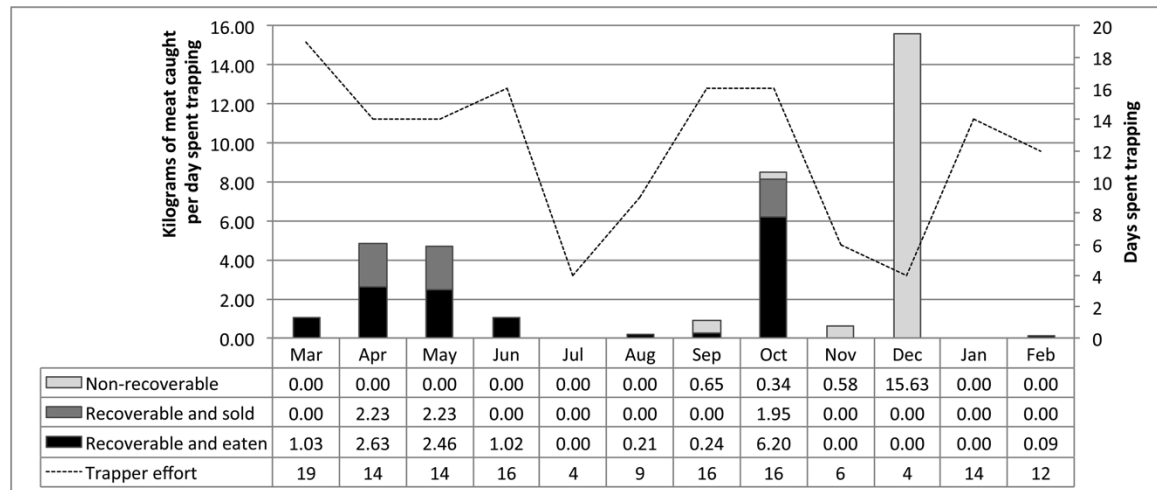


Figure 8. Seasonal variation in the effort and productivity of a focal trapper on the Masoala Peninsula (July 2011 – June 2012). The focal trapper spent 4 – 19 days per month trapping (average =  $12 \pm 5.55$ ) and caught an average of  $0.38 \pm 0.3$  forest mammals or  $3.75 \pm 4.74$  kg of forest mammal meat for every day he trapped. The focal trapper was unable to recover (or eat) an average of  $1.43 \pm 4.48$  kg of forest mammal meat for every day he spent trapping (these animals decomposed or were predated before the trapper returned to check the trap). This non-recoverable or wasted catch was highest in the austral summer.

### Reasons for seasonal hunting

Seasonal changes in hunting patterns on the Masoala were neither driven by seasonal scarcity in sources of animal foods, nor by cultural norms or hunting laws (Table 9). While peak wildlife consumption coincided with seasonal food insecurity, neither domestic animal nor fish consumption could predict wildlife consumption (Table 11). The number of days the trapper spent trapping could also not be predicted by the consumption of alternative animal foods nor the total, recoverable, or unrecoverable (from decomposition) amount of biomass the trapper caught each day (Table 11).



Furthermore, laws that designate the protected status of wildlife species or that specify hunting seasons also had little effect on seasonal patterns of wildlife hunting (Table 8). Almost three quarters (73%) of the forest mammals caught by the village and half (50%) of those caught by the focal hunter, were illegally harvested (either out of season or prohibited). Illegal hunting peaked in the village from January through March when tenrecs were hunted out of season and peaked for the focal hunter in March and June during endangered lemur trapping.

Seasonal hunting was driven by characteristics of the prey that changed throughout the year (Table 9). The most important characteristics were (1) seasonal variation in prey behavior, and (2) seasonal variation in body fat content. Seasonal variation in prey behavior either (a) increased the predictability of the species location (which increased catch per day), or (b) increased the species overlap with humans, crops, or domesticated animals (which increased both catch per day and human-wildlife conflicts) (Table 9).

The predictable locations of euplerids and lemurs were utilized in trapping methods. *Fossa fossana* were trapped on hot 'dry' days in travel paths to, from, and over rivers when water tables were low. *Eulemur albifrons* and *Varecia rubra* were trapped during the winter in travel paths to seasonally fruiting trees, when these animals had their highest quantity of body fat. When the focal trapper trapped large lemurs at seasonally fruiting trees in March and June, he spent 30-58% more days trapping than during the rest of the year (Figure 8). The focal hunter spent fewer days

trapping when he was ill, celebrating holidays, or working for a salary (opportunistic small jobs).

Human-wildlife conflicts drove increased hunting of both euplerids and bushpigs. *Cryptoprocta ferox*, *Galidia elegans*, and *Galidictis fasciata* were caught by villagers in town when they killed poultry in the austral summer and more bushpigs were caught when they consumed tuber crops in the austral winter. While the majority of carnivorans were caught for food during the austral summer (with the exception of most *C. ferox*), all of the carnivorans caught between February and July (*C. ferox*, *G. elegans*, and *G. fasciata*) were caught because of human-wildlife conflict over poultry.

### **The impact of seasonal hunting patterns on wildlife and people**

The consequences of seasonal hunting for the hunted species vary by taxon. Euplerid hunting coincided with these animals' mating, pregnancy, and lactation, greatly increasing the impact of hunting on this taxon. Hunters trapped *Fossa fossana* and *Eupleres goudotii* during pregnancy and lactation. They hunted *Cryptoprocta ferox* during mating season (October through December, when males increase the size of their range), and again after *Cryptoprocta* females give birth to their young and are nursing (March). Hunting of *Tenrec ecaudatus* also coincided with this species' reproduction; entire litters of dependent offspring (14+) are often caught at one time. In contrast, lemur hunting occurred at an optimal time of year when these animals' had weaned their offspring, but had not yet begun mating.

While the seasonal lack of alternative animal-based foods was not the reason why people seasonally hunted more forest mammals, they still ate more forest

mammals during periods when fish and domestic animal consumption was lowest.

Because people targeted bushpigs, tenrecs, and endangered lemurs when other animal foods were scarce, these species may provide more nutritional and economic benefits to local people than those hunted when animal foods are more abundant.

### **Differences between methods**

The three methods of collecting data (focal hunter follows, interviews, and 24-hour recall surveys) produced slightly different results. Most notably, the reports of forest animal consumption from 24-hour recall surveys are likely to underestimate consumption. With the exception of bushpigs, household members rarely reported eating a forest mammal during the 24-hour recall surveys, even if those people were seen eating forest mammals that day. In contrast, all meals I observed containing forest mammals were reported during annual recall interviews. When questioned about this discrepancy, participants revealed that they did not report their consumption of forest mammals during the 24-hour recall surveys because: (1) these surveys were conducted by a Malagasy assistant and it was perceived that they were more likely to share this information if pressured physically by the military after my absence; and (2) the illegal behavior had happened more recently (i.e. within the previous 24-hours) and incriminating evidence of eating an illegal animal (e.g. leftovers, hair, or bones) still may be available

### **Discussion**

Whereas there is a wealth of valuable literature on hunting and the consumption of wild meat (Milner-Gulland et al., 2003; Fa et al., 2006; Brashares et al., 2011; Golden

et al., 2011; Milner-Gulland 2012; Golden et al., 2014), information on seasonality of hunting is currently lacking. By ignoring the seasonality of hunting we risk missing information that could be vital to developing sustainable conservation policies and action plans (Golden et al., 2013). This study's full year (2011-2012) of direct observations of hunting, interviews with villagers, and 24-hour diet recalls suggest that there is seasonal variation in the hunting of forest mammals and the consumption of fish and domesticated livestock on the Masoala. The repercussions of this timing on native euplerid carnivorans may warrant a revision of the conservation status of some species; native euplerid carnivorans may be far more endangered than previously recognized. Additionally, the extent to which seasonal variation in human factors and prey characteristics drive these seasonal hunting patterns reveals that people decide *whether* or not to hunt independently of their decision of *when* to hunt particular species. Finally, our results suggest that conservation efforts for each taxon should be focused on different times of year on the Masoala to optimize their effects.

Unlike studies that rely solely on secondary accounts of hunting and meat consumption collected through interviews and recall surveys, this study also incorporated first-hand observation of the hunting of a focal-individual throughout an entire year. While researchers should be wary of inferring village hunting patterns from observations made on a single individual, such in-depth observations can be extremely valuable. The behavior of this study's focal hunter was consistent with the behavior of other bushpig hunters, as inferred from other hunters' reports during interviews. However, he differed from opportunistic hunters who caught fewer animals, ate less

meat from bushpigs and lemurs, ate more meat from bats, and used slingshots. Once trust has been established, other hunters may be willing to collect accurate daily self-report data in addition to first hand observation of hunting activities. Further, future efforts to understand how hunting varies across the entire peninsula will be essential for designing (and applying) effective regional conservation and public health action plans.

### **The reasons for seasonal hunting patterns**

Hunters targeted endangered lemurs and bushpigs during the cool, wet austral winter (March – August), and ate more native euplerid carnivorans (e.g. *Cryptoprocta ferox*, *Fossa fossana*), introduced viverrids (i.e. *Viverricula indica*), fish, and domesticated livestock during the warm austral summer (September – February). Seasonal increases in hunting coincided with food insecurity within the human community. However, seasonal changes in hunting patterns were neither driven by seasonal scarcity in animal foods, nor by cultural norms or hunting laws. Instead, seasonal hunting was driven by seasonal variation in the ranging behavior, diet, and body fat content of their prey. This study illustrates an important aspect of hunting on the Masoala: the reasons people hunt in general are not the same as the reasons for seasonal patterns in hunting. Hunters maximize their energetic efficiency, hunting animals when they can expend the least amount of energy for the greatest gain, be that gain direct (from eating their meat) or indirect (from saving crops or poultry) (Stephens and Krebs, 1986). If these results are validated elsewhere, conservationists may also be able to apply their knowledge of the seasonal changes in ranging behavior, diet, and fat

storage of endangered species to predict when these animals are most likely to be hunted.

### **The impact of seasonal hunting patterns on native species**

Euplerid and tenrec hunting coincided with these animals' pregnancy and lactation, increasing the impact of hunting on these species. These findings raise particular concern for *Cryptoprocta ferox*, *Fossa fossana*, and *Eupleres goudotii*. People hunted *C. ferox* during mating season (October through December, when males increase the size of their range), and again after *C. ferox* females give birth to their young and are nursing (March). Thus, the hunting of *C. ferox* increased at the two most sensitive times for their reproduction. People also hunted *F. fossana* and *E. goudotii* during pregnancy and lactation. Further, the native *F. fossana* and introduced *V. indica* are caught in the same style of trap. Therefore frequent catch of the introduced *V. indica* can encourage continued trapping effort and continued incidental catch of native *F. fossana*. This may further stress populations of *F. fossana* already reduced from habitat alteration. Native carnivorans are also more likely to decompose in traps than are other native mammals because they are targeted during the hot austral summer when ambient temperatures are highest.

Three native euplerid carnivorans are seasonally hunted because of human-wildlife conflict over poultry: *C. ferox*, *Galidia elegans*, and *Galidictis fasciata*. These results parallel some of the recent findings regarding carnivoran-hunting in central-southeastern Madagascar (Kotschwar Logan et al., 2014), with a few important distinctions. On the Masoala, as in central-southeastern Madagascar, *C. ferox* and *G.*

*elegans* are hunted primarily because of human-wildlife conflict over poultry, but in contrast to central-southeastern Madagascar, *G. fasciata* was also exclusively hunted (albeit less often) on the Masoala when they predated on chicks within the village. Other distinctions include the additional infrequent hunting on the Masoala (but not in central-southeastern Madagascar) of *C. ferox* for food, and the hunting of *V. indica* solely for food. *V. indica*, *F. fossana*, and *E. goudotii* did not predate village poultry. In contrast to Kotschwar Logan et al. (2014), we found that taboos provided little protection to native euplerid carnivorans in this region. The taboos against carnivorans were restricted to the consumption of animals and not their killing. Therefore, people who would not eat *C. ferox*, still kill *C. ferox* when these animals predate their poultry.

The conservation community in Madagascar has tended to focus on the impacts of habitat loss and hunting on Madagascar's endemic lemurs (Borgerson, 2015). We are only beginning to understand the conservation threats euplerids face from hunting, habitat alteration (Gerber et al., 2012; Farris et al, 2014), and the direct (i.e., competition for resources) and indirect (disease transmission) threats from introduced carnivorans (Dollar, 2006; Vanak & Gompper, 2009). The conservation status of many euplerids may need careful re-evaluation. *F. fossana* and *E. goudotii* are currently listed as not threatened and *C. ferox* is listed as vulnerable (IUCN, 2014). The Masoala-Makira landscape is a key conservation area for *C. ferox* and is one of only two forest regions that may contain more than 300 *C. ferox* (Gerber et al., 2012). The population of *C. ferox* within the Masoala-Makira landscape is estimated at approximately 762 individuals (Farris et al., 2014), and four of these individuals were trapped within a

single year in only one of approximately 370 villages surrounding the Masoala and Makira protected areas. Unpublished data (Borgerson) show that the number of *C. ferox* caught within this study year is not atypical.

Our study showed that people hunted lemurs after these animals had weaned their offspring, but prior to their mating season. This limits the impact of hunting on their dependent offspring. However, because people eat more fish and domesticated animals during the austral summer, conservation efforts that aim to reduce the hunting of threatened lemurs on the peninsula by increasing poultry production (Andrianjara et al., 2013) will face challenges. First, poultry are eaten most often during the austral winter when animal foods were most (and not least) abundant. Secondly, poultry and lemur consumption peak during different seasons. Finally, unless efforts to increase the production of poultry also reduce human-carnivore conflicts over poultry, they may unintentionally increase the hunting of native euplerids.

### **The impact of seasonal variation in hunting and meat consumption on people**

While seasonal hunting patterns are not driven by seasonal scarcity of resources on the Masoala, they will still impact the health and livelihoods of hunters. Because people consume more lemurs, bushpigs, and tenrecs when they consume fewer domestic animals and fish, lemurs, bushpigs, and tenrecs may make a greater contribution to human health and nutrition than animals hunted during the austral summer.

If collected sustainably, many wild species could provide valuable renewable sources of fat, protein, and important micro-nutrients for local people. Tenrecs and



bushpigs comprised the most wild meat eaten in number of individuals and biomass, respectively. One hundred and five tenrecs were caught in a single year. Tenrecs are not threatened, and are designated as a game species in Madagascar with a legal hunting season. However, the vast majority of tenrecs caught during this study were hunted outside of the legal hunting season for *Tenrec ecaudatus*, when members of this species are pregnant and lactating. *T. ecaudatus* are prolific breeders (Nicoll, 2003; Racey & Stephenson, 1996), but because people hunt them during critical points in their reproductive cycle, they are unlikely to reach their maximum potential productivity. In fact, the local people report that *T. ecaudatus* populations have drastically declined within the last decade, and they themselves think this may be from their own over-hunting. If hunting patterns shifted to the legal season, so that *T. ecaudatus* were caught only after juveniles gained independence, and if policy efforts are designed to assist population rebound (while considering human incentives, reactions, and long-term consequences), this species could provide significant health and economic benefits to local people.

### **Seasonal timing of conservation and public health policy**

Seasonal hunting and meat consumption on the Masoala Peninsula may amplify both the effect of hunting on native euplerids and tenrecs and the contribution of lemur, bushpig, and tenrec meat to local human health. Conservationists may be able to increase the efficiency of their species action plans on the Masoala Peninsula if they time their efforts to coincide with either the hunting of euplerids during the austral summer, or the hunting of tenrecs and endangered lemurs during the austral winter.

Similarly, efforts to improve the health and welfare of local people may be more effective if they are timed to improve conditions during the austral winter, when people eat fewer alternative animal-based foods. Incorporating an understanding of seasonal patterns of hunting and meat consumption can help us to optimize our efforts to improve the health of local people and native species, strengthening both the design and application of conservation policy.

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## CHAPTER 4

### WHO HUNTS LEMURS AND WHY THEY HUNT THEM

#### Abstract

The main threats against lemurs are habitat loss and hunting. This means we have to work with people and determine *why* people alter their habitats and hunt lemurs. Conservation policies often assume that people will decrease illegal hunting if they know about the laws prohibiting or regulating the hunting of wild animals, are better educated, are involved in ecotourism, have greater access to affordable meat from domesticated animals, are less poor, or are healthier. Yet, we often don't know how or if these factors influence hunting where conservation policies are implemented. Furthermore, we often cannot reliably predict who is most likely to engage in illegal hunting. This chapter aims to address these questions for one of the most biodiverse places on earth, the Masoala Peninsula of Madagascar, where highly endangered lemurs are trapped for food (Chapter 2). I asked members of every one of a focal village's households over 600 questions to answer the following questions: (1) Why do people hunt threatened lemurs? and (2) How do we identify households that are likely to engage in hunting lemurs? We can use this information to design conservation policies that address the causes of lemur hunting and increase the likelihood that combined human-livelihood and conservation efforts actually reach hunters. Of the numerous potential causal factors, those that best predicted a person's decision to engage in illegal hunting were poverty, poor health, and malnutrition of children in the hunter's



household. My results suggest that the welfare of humans and lemurs are linked; the key to discouraging illegal hunting, and improving the future viability of endangered lemur species, may be improving rural human health and welfare.

### **Introduction**

Because humans interact dynamically with ecological systems, a recent crescendo of research advocates collaboration between the social and biophysical sciences (Gibson et al. 2000; Costanza et al. 2001; Ostrom 2005; Milner-Gulland 2012). Madagascar is a global biodiversity hotspot and a priority for conservation (Myers et al. 2000). The island nation is also currently facing a dual crisis for both biodiversity and public health. The country's endemic lemurs are now recognized to be the earth's most endangered mammals (Schwitzer et al. 2013), and the food security of Madagascar's people has plummeted to nearly last in the world (EIU 2014). In the midst of this, endangered lemurs are hunted for food (Chapter 1).

We know that unsustainable hunting can threaten biodiversity, as well as human health and food security (Milner-Gulland et al. 2003; Golden et al. 2011). Thus, sound conservation policy should be grounded in the knowledge of why people choose to hunt endangered animals. Of course, it is not easy to identify or to quantify the reasons people engage in illegal hunting when they have a great stake in keeping such activities hidden (Razafimanahaka et al. 2012). However, collecting these data is essential to devising effective conservation strategies. Conservation efforts will be more effective when they include site-specific policies that address why people hunt wild animals and can identify people who are currently motivated to engage in illegal hunting.

Most forest resources are common-pool goods, both subtractable in consumption and difficult to exclude from potential users, thus challenging to provide and easy to deplete (Ostrom 1990, McKean 2000). Although national governments and international regimes may claim ownership or regulatory rights, local people retain the physical opportunity to utilize the forests and can respect, ignore, or defy the government's laws. Conservation efforts proposed for Madagascar to date propose that we can deter people from illegally hunting endangered species by increasing education and the knowledge of hunting laws (Jenkins et al. 2011; Keane et al. 2011), increasing ecotourism (Schwitzer et al. 2014), alleviating poverty (Sunderland et al. 2005; Garner et al. 2013; Gardner & Davies 2014), and improving domestic animal husbandry (Golden et al. 2011; Razafimanahaka et al. 2012). These assumptions, surprisingly, are often not well tested where conservation policies are implemented, and may not even be correct. How a person's, knowledge or fear of the government's hunting laws, education, wealth, involvement in ecotourism, access to affordable meat from domesticated animals, or family health actually affect the decision to hunt endangered species is simply not known. Without this knowledge, conservationists cannot alter the behavior of those who illegally hunt lemurs.

Within Madagascar, the Masoala Peninsula, a UNESCO world heritage site, is one of the highest priority areas for conservation (Kremen et al. 2008). Despite nearly 20 years of conservation efforts on the peninsula, people still hunt lemurs and other endangered mammals (Chapter 1, Chapter 2). I interviewed every person within a focal village on the peninsula and used the responses to 600 interview questions on behavior,

wealth and food security, health, demographics, value, government regulation of or local community rules concerning food and resources, and human-wildlife questions to answer the following questions:

- (1) Why do people hunt threatened lemurs?
- (2) How do we identify households that are most likely to contain lemur-hunters?

This data will allow us to test the following hypotheses about the proximate and ultimate causes of the decision to hunt lemurs:

- H<sub>1</sub>: Knowledge of law and fear of enforcement: Lemur hunters are unaware of the laws against lemur hunting or of enforcement of these laws, but those who understand the law and fear its enforcement will refrain from hunting lemurs.
- H<sub>2</sub>: Formal education: People with greater formal education will have expanded opportunities for income and employment, so will not need to hunt lemurs as a free food source.
- H<sub>3</sub>: Involvement in ecotourism: People who gain income from ecotourism will prefer to leave lemurs alive in the wild to attract ecotourists to the area so will avoid and discourage hunting them.
- H<sub>4</sub>: Demographic traits of households. We may find that households with more men do more hunting (since only men engage in intentional trapping), or that households with more women do more opportunistic hunting to make up for the relative absence of men bringing in other forms of income, or that households with more people to support, or more children to raise, do more hunting to enlarge the food supply for the household. We may find that in-migration has an impact on lemur hunting. Persons from distant locations may not know much about the supply or methods of hunting lemurs in the Masoala so simply cannot hunt successfully, or persons from distant locations may not honor local customs and taboos on the consumption of certain species so may opt to hunt more than persons of local origin.
- H<sub>5</sub>: Traditional values: Holding traditional values may affect hunting in multiple ways. Lemur-hunting might be a traditional occupation or activity for some households, and traditional values or food cultures may encourage or prohibit certain kinds of hunting.

- H<sub>6</sub>: Opportunity: Livelihood strategies that increase the amount of time spent in the forest may increase the opportunity for hunting.
- H<sub>7</sub>: Taste preferences: Some people may like the taste of certain lemurs over other foods and prefer to hunt them.
- H<sub>8</sub>: Conflict with wildlife species who eat domestic animals and crops: People may hunt more if they see wildlife as a threat to their domestic crops and animals.
- H<sub>9</sub>: Access to alternative meat: People who have a greater access to alternative sources of meat will not hunt lemurs to supplement their diet.
- H<sub>10</sub>: Poverty: People with relatively little wealth and income will hunt lemurs as free supplements to their diet, whereas people with more wealth and income will not need to do this.
- H<sub>11</sub>: Health: People in households whose members are malnourished and fall ill frequently will be more likely to hunt lemurs as an important dietary supplement than will people in better health.

## **Methods**

### **Study Site and Data Collection**

This study took place over twelve consecutive months (July 2011 – June 2012) in a focal village on the Masoala Peninsula. I selected the village after completing a rapid assessment of resource use in 36 villages bordering the Masoala National Park. I chose this village as the study site because of its proximity to the park and the strong trust relationship that I had established with members of this community during previous research. There are 10 species of lemurs at the study site (*Varecia rubra*, *Eulemur albifrons*, *Haplemur griseus*, *Microcebus rufus*, *Allocebus trichotis*, *Cheirogaleus medius*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, and *Daubentonia madagascariensis*); 50% of these species are endangered or critically endangered and 90% are threatened (IUCN 2014). *E. albifrons*, *V. rubra*, *H. griseus*, and *C. medius* are hunted most frequently (Chapter 2).

I speak the local dialect of Betsimisaraka and did extensive structured interviews of community members and extensive unstructured interviews of a focal trapper during 12 months of trapper shadowing. I interviewed at least one member of every household (N = 36), and conducted follow-up interviews with every person (N = 112) in the village. I defined households as units comprising all people who shared the use of a single kitchen. I defined adults as individuals 18 years and older, and children as individuals less than 18 years of age. I selected participants for the household interviews based on their availability and therefore included both men and women. I obtained informed consent from all participants. Interviews included over 600 questions about behavior and potential incentives for resource use, at both individual and household levels. These variables allow me to test many of the assertions found in the literature to date about illegal hunting of endangered species, including wealth, health, demographics, opinions, human-wildlife conflicts, education, official and informal regulation of resources (if any), and extraction, consumption, and use of both forest and marine products (Table 12). Interviews lasted between four and twelve hours over the course of one to two days, and were punctuated with frequent breaks.

### **Data Analysis**

I used multiple and bivariate nominal logistic regression analysis to test the impact of wealth and food security, health, demographics, opinions, human-wildlife conflicts, and official and informal regulation of resources (Table 12) on the individual decision to trap lemurs. I then used cluster analysis to characterize groups of people according to whether they trap lemurs or not and then to test how well the various

factors that are often proposed to cause trapping actually do predict trapping. Finally, I employed partition analysis to identify the best indicator or proxy measure of a person's decision to trap lemurs. I defined active lemur trappers as people who had intentionally trapped and caught lemurs within the prior year.

To assess human health, I calculated z-scores for the heights, weights, and body mass indices (BMI) for all children using the CDCs standards for child growth and development (2000) for children over age two. Because reference data on children under age two are not available from the CDC, I used WHO (2006) standards for these children. These standards consider children to be stunted, underweight, or to have a severely low BMI if the z-scores for these variables were more than two standard deviations below the mean (WHO 2006; CDC 2000).

### **Results**

While both men and women opportunistically hunted forest mammals when these animals were encountered, all active trappers were men. Most households had members who had hunted a forest mammal in the prior year, but fewer households had members who were lemur trappers (Table 13). While nearly all men and the members of the vast majority of households had eaten lemur meat within their lifetime, just over one third of men and households reported eating lemur meat in the last year (Table 13). Just under half of all men had trapped a forest animal in the prior year and twenty-six percent of men had intentionally set traps for and caught lemurs (Table 13). All lemur trappers were subsistence trappers; they did not sell lemur meat.

Table 12. Interview and analysis variables used to identify lemur-trappers and to isolate the best predictors of a person's decision to trap lemurs.

Household Interview Topics	Variables Coded for Data Analysis
<b><i>Behavior: Extraction, Consumption, &amp; Use of Forest and Marine Product</i></b>	
For 28 forest mammals, 78 bird species, 5 endangered marine species, and 11 domestic animals, if they had eaten the animal, trapped the animal, if they would eat again, if they would trap again, and the number of each species eaten, caught (and method), bought (cost), and sold (price) last year	Total number of forest mammals (individuals) eaten <sup>†</sup> and total number caught <sup>‡</sup> last year per household and adult man. Number of lemurs <sup>§</sup> , tenrecs <sup>†</sup> , bats*, bushpigs <sup>§</sup> , euplerids*, and viverrids <sup>‡</sup> caught last year. Number of lemurs <sup>†</sup> , tenrecs, bats <sup>†</sup> , bushpigs*, euplerids, and viverrids <sup>‡</sup> eaten last year. Whether members of households and adult men had, in the last year, eaten forest animals, hunted forest animals <sup>†</sup> , trapped forest animals <sup>§</sup> , eaten lemur <sup>†</sup> , hunted lemurs <sup>§</sup> , or trapped lemurs <sup>§</sup> . If they had eaten an endangered forest animal in the last year (binary), endangered marine animal in the last year (binary), if they would eat an endangered forest or marine animal if presented with an opportunity (binary), and the total number eaten*
Extraction of all forest and marine products (days spent collecting, distance, product, number collected, seasonal variation etc.) and the percentage of all forest products sold and for personal use (Forest: timber, precious woods, firewood, animal foods [meat], vegetable foods [wild potato, palm hearts, etc.], honey, bilahy [for alcohol production], medicinal plants, and other. Marine: vertebrate and invertebrate marine animals for food [from line fishing, net fishing, spear fishing, hand collection, and snorkeling subcategories] and animal products for export [sea cucumber].)	Extractive activities (Total N days spent collecting per month* and total per category) (significant categories: animal foods [meat]) <sup>‡</sup> , whether they had engaged in extractive activity from the ocean (binary), whether they sold the marine products they collected*, number of days they spent collecting per month, whether they had from the forest (binary), number of days per month, whether they had engaged in extractive activities within the national park (binary), number of days, whether this behavior was illegal, whether extractive activities were primarily for subsistence or sale, percentage of forest, marine, and park products sold, cash value of forest, marine, and park products sold
Percentage of raised/hunted/fished domestic, forest, and marine animals sold and eaten (cost)	Whether they sold their domestic, forest, and marine animals (binary), percentage sold and eaten, income earned
How these percentages had changed over the previous 15 years	Whether reliance on domestic, forest, and marine animals had increased, decreased, or remained the same over the previous 15 years

<b><i>Institutions &amp; Resource Regulation</i></b>	
Knowledge and understanding of governments laws on lemur hunting	Knowledge and understanding of governments laws on lemur hunting
Existence of informal local rules on lemur hunting	Existence of informal local rules on lemur hunting
Perception of laws made locally and not locally	Perception of laws made locally and not locally
Law adherence	Whether they had engaged, in the last year, in illegal behavior in general, within the forest gathering non-food forest products, within the forest gathering food products, and within the ocean, and whether they earned money from each of these behaviors
Ownership of forest and ocean	Ownership of forest and ocean
Responsible party for protecting/maintaining the forest and ocean	Responsible party for protecting/maintaining the forest and ocean
For all animal foods that were not eaten, participants were asked whether this was because of laws, tourism, fady, dislike in taste, inedibility, or another reason	Percentage of forest mammals not eaten because of laws, tourism, <i>fady</i> , dislike in taste or size, or inedibility
<b><i>Education</i></b>	
Years of formal education	The number of years of formal education per individual and mean years per household member
<b><i>Ecotourism</i></b>	
Employment (past or present) in eco-tourism (as a guide or at an eco-lodge)	Participation in eco-tourism (past or present employment as a guide or at an eco-lodge)
Number of people within the household employed in ecotourism	Number of people within the household employed in ecotourism
Income earned from employment in ecotourism	Income earned from employment in ecotourism
Indirect gains from ecotourism (e.g. selling crafts or singing for tourists)	Indirect gains from ecotourism (e.g. selling crafts or singing for tourists)
Income earned indirectly from ecotourism	Income earned indirectly from ecotourism
<b><i>Demographic Traits of Household Members</i></b>	
Number of household members	Number of household members
Age of each household member	Individual and mean household age
Sex of each household member	Household sex ratio
Number of biological children	Number of biological children, presence of children within their household
Birthplace	Individual and mean household distance of adult birthplace (scaled 1-3)



<b>Human-Wildlife Conflicts</b>	
The number (and species) of animals that stole their food in the last year	The number of wild animals that 'stole' their food in the last year
The action taken and result (i.e. were they trapped? caught? Etc.)	The number of those animals they trapped as a result of this 'theft'
Rank the top three animals they perceived as being a greatest threat to their livelihood	Whether they listed a lemur or a bushpig as a pest, whether they had experienced a conflict with a bushpig or a lemur in the last year
<b>Access to Alternative Animal-Foods</b>	
Livestock ownership	Total N of livestock, cows, pigs, poultry, chickens, geese, ducks, dogs, cats
Livestock consumption	Total number of times all domestic animals were eaten in the last year, number of times poultry were eaten
Collection of marine animal foods	Days per month spent fishing/collecting
<b>Wealth</b>	
Number of houses	Number of houses <sup>†</sup>
The number of rooms in each house	Number of rooms per household member
The material these houses were constructed from	Housing material and size score <sup>†</sup> (Sum materials score of housing materials and number of rooms for all buildings in household) Roof (2 insulated, 1 sheet metal, -1 forest product, -2 no/partial roof) Walls (2 insulated, 1 board, -1 falafa/bamboo, -2 no/partial walls) Flooring (2 concrete/linoleum, 1 board, -1 konko/bamboo, -2 dirt)
Income	Total household and individual income, income from different livelihood strategies
Household expenditures	Household expenditures per person per day Household expenditures purchased locally per person per week Household expenditures purchased in another town per person per month
Number of household members with daily cash income	Number of household members with daily cash income
The cost of all health care	The cost of individual health care and mean cost per person per household
<b>Health</b>	
Height	Individual adult male and mean child z-scores for height for age
Weight	Individual adult male z-scores for wt for age and bmi for age Mean household child z-scores for wt for age and bmi for age* (z-scores derived from WHO and CDC)
Number of days they were sick in the last month	Mean and individual number of days they were sick in the last month
Number of days they were sick in the last year	Mean and individual number of days they were sick in the last year
Bivariate nominal logistic regressions reveal that this variable can significantly predict a man's decision to hunt lemurs at the * (P < 0.05), † (P < 0.01), ‡ (P < 0.001), or § (P < 0.0001) level.	

Table 13. The frequency of lemur consumption and trapping among households and men in a focal village on the Masoala Peninsula (2011-2012). While both men and women hunted, only men were active trappers.

	Lemur consumption		Hunting in the prior year			
	<i>Had ever eaten in their lifetime</i>	<i>Ate in last year</i>	<i>Hunted forest mammals</i>	<i>Trapped forest mammals</i>	<i>Caught a lemur</i>	<i>Intentionally trapped lemurs</i>
<b>Percentage of Households (N = 36)</b>	89	36	75	36	33	22
<b>Percentage of Adult Men (N = 34)</b>	91	35	70	43 <sup>b</sup>	35	26 <sup>b</sup>

<sup>a</sup> Intentionally, opportunistically, or as by-catch

<sup>b</sup> I was unable to interview three men about their trapping behavior because they were away from the village during the time of interviews (N = 31)

I identified 23 significant predictors of lemur trapping, all in the categories of “Behavior”, “Wealth”, and “Health” (see Table 12 for all groupings of variables into categories). None of the variables within the other categories was a significant predictor of the individual’s decision to trap lemurs. For example, the trapping of lemurs could not be predicted by a person’s employment in ecotourism (bivariate nominal logistic fit:  $\chi^2 = 0.37$ ,  $DF = 1$ ,  $P = 0.54$ ), the number of years he went to school ( $r^2 = 0.09$ ,  $DF=1$ ,  $\chi^2 = 3.06$ ,  $P = 0.08$ ), or his ownership of livestock ( $r^2 = 0.04$ ,  $DF = 1$ ,  $\chi^2 = 1.51$ ,  $P = 0.22$ ) or poultry ( $r^2 = 0.03$ ,  $DF = 1$ ,  $\chi^2 = 1.15$ ,  $P = 0.28$ ).

The three best predictors of a person’s decision to trap lemurs were: (1) the number of days he was sick in the prior month; (2) the materials and size (number of rooms) of his home; and (3) the average z-score of the children’s body mass indices (BMI) per age in his household. When included in regression models these three variables masked the effects of all others. Together these three variables explained 69.58% of the variation in whether a man had trapped lemurs in the last year (multiple nominal logistic fit:  $R^2 = 0.696$ ,  $DF=3$ ,  $\chi^2 = 18.369$ ,  $P = 0.0004$ ). A discriminant function analysis using these variables misclassified only three lemur trappers (13%).

In comparison to those who did not hunt, lemur trappers were, on average, sick twice as long (12 vs. 6 days) in the previous month as men who had not trapped lemurs. Lemur trappers also had smaller homes built of non-timber forest products rather than of boards and metal. Mean child z-scores for BMI for age were significantly lower within the households of men who trapped lemurs (-1.33 [1.03] vs. 0.45 [0.92], t-test:  $t = -1.87$ ,

DF = 14.69, P = 0.049). Within the entire village, stunted and underweight children were quite prevalent (Figure 9), but children who were stunted, underweight, or had severely low BMI for their age were more prevalent in households that trapped lemurs than in those that did not (Figure 9).

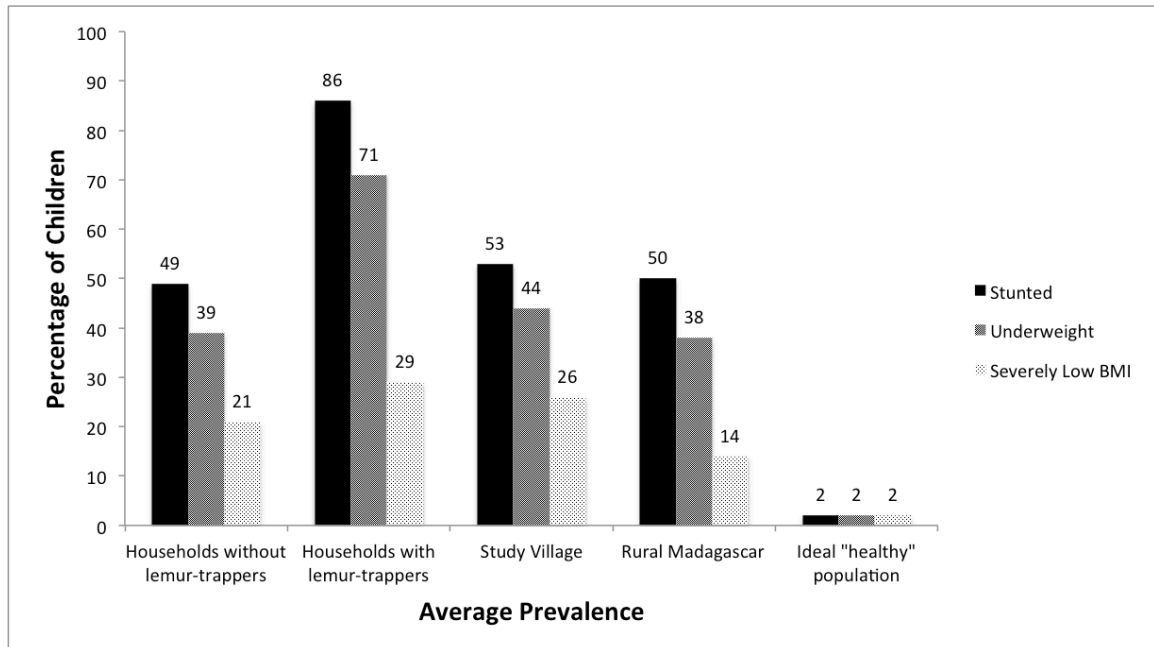


Figure 9. A comparison of child malnutrition between those households that trapped lemurs and those that did not trap lemurs in a focal site on the Masoala Peninsula of Madagascar (2011-2012).

I used partition analysis to identify non-sensitive survey questions that would best identify or predict which households contained lemur-hunters. Two of the over 600 interview topics could accurately identify 64.5% of the people who trapped lemurs: (1) Did they trap last year?; and (2) Did they catch one or more bushpigs last year? ( $R^2 = 0.645$ , Number of splits = 2, AICc = 63.484). That is, most people who illegally trapped lemurs also legally trapped bushpigs.

## **Discussion**

This study of illegal lemur hunting in a biodiverse region of rural Madagascar identifies poverty and poor health as the strongest drivers of the illegal trapping of lemurs. Most of the households at our study site on the Masoala hunt forest mammals (75%) and over a third (36%) eat lemurs. This hunting, given the insecure future of both lemur populations and the food security of Madagascar's people (IUCN 2014; EIU 2014), warrants the attention of those working in both the fields of conservation and of public health. Numerous agencies have worked to secure the future of both lemurs and people on the Masoala Peninsula. Yet, despite nearly 20 years of conservation efforts, more than a quarter of all men (26%) at our site trapped lemurs, and child malnutrition remains very high (86% of children in lemur hunting households). For a conservation policy to be effective in a region where illegal hunting occurs, it must be able both to reach the actual lemur-hunters and to address the causes and motivations for hunting lemurs.

### **Testing hypotheses about interventions and lemur-hunting**

Poor people were more likely to hunt lemurs than 'wealthy' people within the focal village. These findings support those of Brashares et al. (2011), which indicate that in rural settings, poorer households consume the most wild meat. Rural economic development and other efforts to alleviate poverty in regions with high biodiversity may provide alternative livelihoods for hunters, increasing the accessibility and affordability of alternative meats and decreasing the rural subsistence-hunting of endangered species (de Merode et al. 2004).

While we found that neither ownership of poultry nor other livestock could accurately predict lemur-hunting decisions, lemur trappers did own fewer livestock than those who obeyed the legal prohibitions against hunting lemurs. Ownership of alternative sources of animal foods may not have discouraged illegal hunting of lemurs for meat in our study, perhaps due to small sample size, but also for several substantive reasons. Poultry die from Newcastle disease at high rates, eviscerating the investment in keeping poultry, and wiping out the expected long-term supply of alternative meat. Poultry and lemurs are eaten during different seasons (Chapter 3), so a supply of poultry eaten during summer may not suppress the drive to hunt lemurs during the austral winter. Poultry may also not be fully substitutable for lemur meat because of complex perceptions about fat, taste, variety, role in local food traditions, or the feeling of fullness that eating lemur meat reportedly provides. Finally, hunting households may simply be too poor to invest in enough poultry to replace lemur-hunting. If conservation policies providing poultry could address the potentially confounding elements of disease, household poverty, and seasonal variation in availability of different meats, then improving domestic animal husbandry for alternative meats might yet provide a direct means of increasing both the accessibility and affordability of meat protein while alleviating pressure on endangered species (Apaza et al. 2002). Further research is needed on the root causes of food insecurity and poverty, the precise mechanisms through which these factors affect human health, and the hunters' perceptions of possible and actual alternatives to illegal hunting.

Ecotourism is often cited as an ideal conservation strategy because it is thought to combine bottom-up and top-down approaches to wildlife conservation and improve local livelihoods (Gössling 1999; Kiss 2004). Its proponents argue that it gives local residents a powerful incentive to maintain living populations of the wildlife and habitats that attract ecotourists, and reduces the incentive to extract flora and fauna for consumption or for income. However, ecotourism as actually practiced can also fail to improve human livelihoods and fail to influence resource use (Kiss 2004; Spiteri & Nepal 2006; Waylen et al. 2009). Our results also show that, at this site on the Masoala, ecotourism fails to reduce the illegal hunting of lemurs; neither involvement in ecotourism nor amount of income derived from ecotourism had any impact on decisions to hunt lemurs. In fact, households with more members working in ecotourism contained slightly more lemur trappers.

Similarly, knowledge of laws and government behavior had no impact on the individual decision to hunt, trap, or consume lemurs. Both lemur-hunters and those who did not hunt lemurs had virtually identical understandings of the content of lemur hunting laws and beliefs and fears about vigorous enforcement and severe punishment for violators. Keane et al. (2011) have found that involvement in tourism can increase an individual's knowledge of the government's wildlife laws to protect the endangered species upon which ecotourism depends. But, our data show that, at this site, those involved in ecotourism and those who were not involved had the same understanding of (albeit simple) lemur-hunting laws, which in turn had no effect on the decision to hunt lemurs.

Because this study examined variations in behavior within and not between villages, we may not see the possible impact of ecotourism and poultry ownership unless we examine data from a regional scale. Further research is needed across the region to increase sample sizes and examine how geographic variables more broadly affect the incentives to trap lemurs and our ability to predict who traps lemurs. However, given our findings from the Masoala and the growing literature questioning ecotourism's impact on human livelihoods (Kiss 2004; Spiteri & Nepal 2006; Waylen et al. 2009), closer scrutiny of the potential for ecotourism to reduce illegal trapping may be warranted.

### **Why do people illegally hunt threatened lemurs?**

The best predictors and strongest drivers of a hunter's decision to trap lemurs were poverty and poor household health. The children within the households of men who trapped lemurs were more stunted and underweight than those in households who obeyed legal prohibitions on the hunting of lemurs; almost all children in lemur hunting households were stunted and most were severely underweight. Given the already high prevalence of malnourishment and poor growth among all of the children in the village, these findings are alarming. Our findings support those of Golden et al. (2011; 2014), which illustrate the benefits of wildlife consumption to child health and household economy. Unless lemur conservation efforts on the Masoala prioritize child health, they are unlikely to have the desired long-term effects. Indeed, ill-considered conservation policies may generate the opposite outcome if they instead disproportionately damage households already experiencing the most severe malnourishment. If the benefits of



these policies fall instead on the wealthier households that do not hunt lemurs now, and instead drive the lemur-hunting households further into poverty and poor health, these policies will actually increase the incentives for those households to illegally hunt lemurs.

### **How do we identify households that are most likely to contain lemur-hunters?**

Even a well-designed conservation and human health action plan that addresses the incentives of hunters may fail if it does not address and alter the factors that drive people to trap lemurs. Lemur-trappers are reluctant to disclose themselves, even to members of their own village. Therefore, it makes little sense for a conservation initiative to attempt to identify the households whose livelihood strategies they want to change by directly asking households to reveal whether they trap lemurs. Our results found that two less sensitive questions could accurately predict a high proportion of lemur trappers: (1) did you eat bushpig meat in the last year?, and (2) did you catch this bushpig yourself? The ability to reliably and rapidly predict who is most likely to illegally trap lemurs would help ensure that people who are not lemur trappers (i.e. the relatively secure and healthy) do not monopolize benefits from conservation programs because of their greater social and economic ability to take advantage of them. If projects to improve the health and livelihoods of rural villagers as a way of reducing the incentive or motivation for hunting lemurs prioritize reaching the households of bushpig-hunters (who are so likely to hunt lemurs as well), then such policies may be somewhat effective at reducing the subsistence trapping of lemurs. Conversely, however, efforts to offset the hunting of lemurs by encouraging the legal hunting of

introduced bushpigs (as suggested in Andrianjakarivelo, 2000) may unintentionally increase illegal trapping of lemurs.

Cooperation among hunters, researchers, policy makers, and implementers in developing conservation and public health action is essential. Because of the strong relationship between an individual's decision to illegally trap lemurs and his wealth, health, and the health of the children in his household, I recommend that conservation and human health initiatives combine their efforts and make improving rural welfare and child health a central component of lemur conservation on the Masoala Peninsula.

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## CHAPTER 5

### A SYSTEM DYNAMICS APPROACH TO ENDANGERED LEMUR CONSERVATION ON THE MASOALA PENINSULA OF MADAGASCAR

#### Introduction

Primates are important flagship and indicator species within conservation management (Durbin et al. 2003). Yet, nearly fifty percent of non-human primates are threatened with extinction (IUCN 2009). It is challenging to develop conservation strategies and even when conservation strategies are developed and implemented, their goals are often difficult to attain. There is a need for fresh approaches to incorporating dynamic information into primate conservation. In order to ensure that conservation attempts promote, and not threaten, sustainable natural resource systems, we must understand the ecology of primates within a human-wildlife framework. This paper will investigate how the application of systems analysis and modeling can advance the field of primate conservation by providing a greater understanding of complex human-wildlife systems. Specifically, we focus on two endangered lemur species (*Varecia rubra* and *Eulemur albifrons*), forest habitats, and human health and wealth at a focal site on the Masoala Peninsula of Madagascar. Using this information we can simulate the complex interactions between nonhuman primates and humans, thus enhancing our ability to predict the sustainability of behavior and the future of endangered primate species.

### **Benefits of a systems approach to primate conservation**

One of the goals of primatology is to empower conservation officials by providing science-based information that informs conservation policies. System dynamics models are frequently used in biology, ecology, policy analysis, and environmental management (Chang et al. 2008, Cockerill et al. 2006, 2009, Costanza and Ruth 1998, Harvey and Klopfenstein 2001, Imam et al. 2009, Leal et al. 2006, Winz et al. 2009). For example, Chang et al. (2008) developed a system dynamics model using Stella (isee systems 2007) to explore integrated approaches to sustainable coral reef management. Their model provided a user-friendly platform that collated published socioeconomic, ecological, and environmental data on Kenting coastal zone in southern Taiwan. Several management scenario analyses were simulated, and four critical sustainable management strategy variables were identified: land development, wastewater treatment, local fish consumption rate, and entrance fee collection (Chang et al. 2008). A system dynamics approach similar to this could be used to develop sustainable management strategies for primate conservation in human-primate systems. The integrated approach and user friendly platform can allow decision makers to simulate the long term effects of proposed conservation scenarios on primates, their habitat, and local human communities before they are implemented.

The inclusion of dynamic systems modeling within primate conservation has many potential advantages. First, modeling can facilitate an increased understanding of the complexity, organization, and interrelatedness of primate, habitat, climate, and human



dimensions subsystems, within the emergent primate system. Primatological systems, like all ecological systems, are subject to a variety of ecological feedback loops that interrelate the biological and ecological aspects of the system, including those between primate species and: (1) primate sociodemographics (Boesch 1996, Chapman and Pavelka 2005, Treves and Chapman 1996) (2) sympatric species (Schreier et al. 2009), (3) habitat (Aureli et al. 2008, Chapman 1990, Chapman et al. 1995, Wrangham et al. 1993), (4) climate (Jolly et al. 2002, Ratsimbazafy 2002a, 2002b, O'Brien et al. 2003), and (5) the interface between human and ecological systems (Lehman et al. 2006a, 2006b, Balko and Underwood 2005, Kumpel et al. 2008, White et al. 1995). The application of computer-based simulation modeling to primatology allows us to develop, test, and revise hypotheses about primate population viability and primate relationships within a complex interrelated system.

Second, computer modeling can promote and increased understandings of complex policy issues, as well as promote agreement and interdisciplinary cooperation between scientists, policy makers, and the public (Cockerill et al. 2004, Cockerill et al. 2009). The visual nature of comparative time simulations is intuitive and compelling. Model simulations also allow researchers to display the delayed effects of long term non-linear relationships, discouraging expectations for instantaneous cause and effect relationships and illustrating the long term, short term, and unintended consequences of current actions.

Third, system dynamics modeling can assist in the development of effective and attainable conservation policy by evaluating current and future conservation strategies,

and ensuring that they support and not threaten sustainable resource use. Primate populations can be simulated over time and under various “what if” scenarios in order to draw conclusions and make decisions about their viability under different management options. Different conservation scenarios (including increased law enforcement, ecotourism, education, alternative protein access, or alternative sources of income) can each be simulated, enabling the researcher to critically assess the potential effects of various conservation strategies on human livelihoods and long-term primate viability. By running these simulations, the social and ecological variables that are most critical in influencing primate population viability can be identified, the sustainability of current human behaviors and future trends in primate viability can be simulated under alternative ecological and behavioral scenarios, and the efficacy and consequences of potential conservation strategies can be simulated. One variable can be controlled at a time and multiple experiments can be run at no additional cost and in little time.

### **Computer-based system dynamics modeling**

Computer-based system dynamics modeling is the quantitative application of a systems approach. The process of building a computer-based model allows the researcher to translate vague statements about how variables interrelate (e.g. logging reduces population size) into explicit mathematical statements of causal relationships. These mathematical statements are based on either field data that the researcher has collected, or that is already available within published literature.

In order to synthesize and keep track of the complex interactions and dynamic behavior that result from the long-term interactions of primate subsystems, dynamic computer modeling is necessary. Computer modeling facilitates the creation of a user-friendly interface that facilitates effective scenario analysis for conservation management. This powerful tool has been successfully utilized in natural resources management to increase awareness of ecosystem-wide ecological interactions, estimate the cumulative impacts of human activities on ecosystems, and evaluate future ecosystem viability through the simulation of “what if” scenarios (Nobre et al. 2010).

Instead of modeling individual behaviors, system dynamics models are composed of complex interacting feedback loops that are analyzed at an aggregate level (Forrester 1969, Richardson 1991, Scholl 2001). Observed discrete events and individual behaviors are seen as symptoms of an underlying dynamic pattern of interactions that drive system behavior. Thus, system dynamics modeling aims to uncover the ultimate causes of system behavior. This holistic approach aims to identify key variables within the defined system. These variables are modeled as stocks or flows. Stocks are variables within the system that can accumulate or decrease, and can be thought of as the reservoirs of the system, e.g. habitat, species population, human population, and aggregates of human actors. Flows are variables that cause these stock conditions to change, e.g. weather patterns, mortality, natality, economy, and culture. Flows can be simply divided into inputs and outputs, or variables that cause the stock to either increase or decrease. For example, within the stock variable of a primate species, inputs may include natality and immigration, whereas outputs might include flows of natural,

resource-based, or human induced mortality. These flows will be characterized by a wide variety of unique system controls, including both physical and cultural rules that will constrain system behavior and influence the ways in which energy is transferred throughout the complex primate-ecological-human system. Once the system's essential variables are identified, the modeler seeks to accurately and quantitatively represent the attributes of and interactions between these variables using differential equations (for more detailed information on the practice of model building see Grant et al. 1997).

The effects of the relationships between these variables are then simulated over time and under various “what if” scenarios. This provides greater insight into the system, and allows for the researcher to draw conclusions and reach decisions. This deductive approach to simulation modeling is highly useful for identifying decisions that can affect system behavior in desired ways. It can, however, also be difficult to determine the feedback loops that are essential to the system and find peer consensus on this feedback structure (Scholl 2001).

### **Goals**

We embraced a systems approach to examine primate, habitat, and human system behavior in one of the world’s most biodiverse places, the Masoala Peninsula of Madagascar (Kremen et al., 1999; Kremen et al., 1998). We modeled the complex interactions of humans, two species of endangered lemur (*Varecia rubra* and *Eulemur albifrons*), and habitat using a year-long data set on human hunting, habitat quality, and lemur density at a single site on the Masoala peninsula (Chapters 2, 3, and 4). Using this model we: (1) estimate *Varecia rubra* and *Eulemur albifrons* population viability at the

study site; (2) identify the social variables most critical in influencing local lemur population viability; (3) evaluate sustainability and future trends in lemur population viability under alternative hunting and behavioral scenarios; (4) begin to examine the challenges conservationists will face in the region by simulating the efficacy and consequences of potential conservation strategies; and (5) identify gaps in our knowledge and suggest future avenues of policy-relevant research.

### **Background Information**

The Masoala Peninsula contains the Masoala National Park, a wet, mountainous, remote UNESCO World heritage site. This park contains most of the remaining lowland coastal rainforest in Madagascar (Kremen et al., 1998). The annual rate of deforestation and disturbance within the Masoala National Park is 1.27% (Allnutt et al. 2013), which is thirty percent higher than the average rate of deforestation within all of Madagascar (Harper et al. 2008). The park protects ten species of lemurs, including *Varecia rubra* (the red-ruffed lemur, Critically Endangered, IUCN 2014) and *Eulemur albifrons* (the white-fronted brown lemur, Endangered, IUCN 2014). The area surrounding the park has 250 permanent villages with a total population of more than 85,000 people (Holmes, 2007). The system we modeled contains: (1) 10 km<sup>2</sup> of “disturbed” habitat bordering the village and Masoala National Park; (2) 10 km<sup>2</sup> of “undisturbed” habitat within Masoala National Park; and (3) a small village (population of 118 in 2012, 149 in 2014), located on the coast, and less than 2 km from Masoala National Park. In addition to subsistence agricultural activities, the local people supplement their income with cash crops (including vanilla and cloves) and illegally harvest timber and sea cucumbers

for export. They fish and supplement their diet with domesticated livestock and forest animals (Chapter 3).

Ninety-seven percent of households in the village consume some forest meat (Chapter 3). This hunting and the alteration of local habitat shapes the local lemur communities in species-specific ways. While alteration of habitat has a greater effect than snare trapping on the populations of *V. rubra*, snare trapping has a greater effect than habitat on the populations of *E. albifrons* (Chapter 2). Villagers caught 292 forest mammals in 2011; 26% of these were lemurs. *E. albifrons* was the most frequently caught lemur (48% of caught lemurs), followed by *V. rubra* (25% of caught lemurs) (Chapter 3). Forest animals were caught largely for individual consumption, and are not intended for sale or economic gain. The primary incentive for illegally trapping endangered lemurs was poverty, poor health, and child malnutrition (Chapter 4). Notably, working in ecotourism has no impact on either the decision to trap or the number of times a person reported eating endangered species over the last year (Chapter 4).

## **Methods**

### **Data Collection**

We used three methods to collect the data for this model: (1) lemur surveys; (2) habitat sampling; and (3) focal-hunter shadowing and extensive interviews. We surveyed lemurs using distance sampling methods (Buckland et al. 1993; Buckland et al. 2001) in twenty 500 m (range = 459-983 m, mean = 620.85 m) triangular transects over one year (July 2011- June 2012) (Chapter 2). We sampled habitat in 60 20m diameter

forest plots located near the corner of each of the triangular transects (Chapter 2). I speak the local dialect of Betsimisaraka and used both direct (hunter shadowing of a focal hunter over one year) and indirect methods (annual recall interviews and 24 hour recall surveys of 100% of village households and all lemur trappers) to determine the intensity of the snare trapping of *Varecia rubra* and *Eulemur albifrons* (Chapters 2 and 3). I also used the extensive interviews and measurements of human health to examine the impact human socioeconomics, health and welfare, micro- and macro-institutions, and behavior and experience have on lemur hunting (Chapter 4).

### **Conceptual Model**

In order to consider the feedback loops between primates, habitat, and local people, we incorporated three subsystems into our model: (1) a “disturbed” subsystem bordering both the National Park and the village; (2) an “undisturbed” subsystem within the Masoala National Park bordering the “disturbed” subsystem; and (3) a human village subsystem (Figure 10). These subsystems are linked together to represent the underlying dynamic pattern of interactions that drives total system behavior.

### **“Disturbed” and “undisturbed” habitat and lemur subsystems**

#### **Habitat**

For the purpose of our model, habitat is the ecological area that influences, and is influenced by, the focal species. Habitat both affects and can be affected by human dynamics and primate populations. Habitat similarly affects humans by regulating water supplies (Nunez et al. 2006), controlling erosion (Zhao et al. 2009), providing medicine (Golden et al. 2012), reducing disease (Myers et al. 2013), and providing essential

timber and non-timber forest products (Byron and Arnold 1999). Habitat also substantially affects primate populations. Primate grouping patterns, range use, mating behavior, dispersal patterns, and social relationships has all been described as adaptive responses to the regional ecological and social environment (Aureli et al. 2008).

We incorporated aspects that may impact humans and primates within our “disturbed” and “undisturbed” habitat subsystems, including: baseline habitat quality (Chapter 2); natural rates of regeneration and decline; measured rates of deforestation and habitat alteration outside of the park; and rates of habitat loss within the park (Allnutt et al. 2013).

### **Endangered Lemurs**

Primate population size is affected by each species’ unique rates of mortality, natality, immigration, and emigration. These rates can be internally influenced by aspects of biology (e.g. maximum birth rates) and social organization (e.g. sociodemographics [Boesch 1996, Chapman and Pavelka 2005, Treves and Chapman 1996]), or externally influenced by habitat or human dynamics. We included elements potentially affecting the population sizes of two primate species (*Varecia rubra* and *Eulemur albifrons*), such as maximum and habitat restricted natality, mortality, and emigration (Rakotondratsima and Kremen 2001, Vasey 2000, 2002); subsistence trapping outside of the park by local villagers (Chapter 3), and gun hunting within the park by people who are not members of the village (this study).

### **Human village subsystem**

Humans can have a substantial effect on both habitat and primates. Human



dynamics can directly affect habitat through the extraction of plants for wood, housing, nutrition, and fuel (Byron and Arnold 1999), and the alteration of habitat for human settlement, infrastructure, and agriculture (Sanderson et al. 2002). Human dynamics can also affect primate population size directly through hunting (Fa et al. 2002b, Kumpel et al. 2008) and indirectly by altering shared habitat (Isaac and Cowlishaw 2004).

Elements of human dynamics that impact habitat and primates were incorporated into the conceptual model. We particularly focused on human factors that may impact the incentive to illegally trap lemurs (Chapter 4), including socioeconomics (e.g. household income, employment, poverty/wealth, immigration); health and welfare (e.g. education, adult morbidity, family planning, child growth, disease, access to medicinal plants for treating disease, access and consumption of alternative meats); micro- and macro- institutions (e.g. governance, ecotourism, regulation, enforcement, compliance); behavior and experience (e.g. human-wildlife conflicts, hunter effort, supply of and demand for lemurs, involvement in illegal logging and/or sea cucumber collection); and the effect these factors have on each other, the hunting of lemurs, and the alteration of habitat.

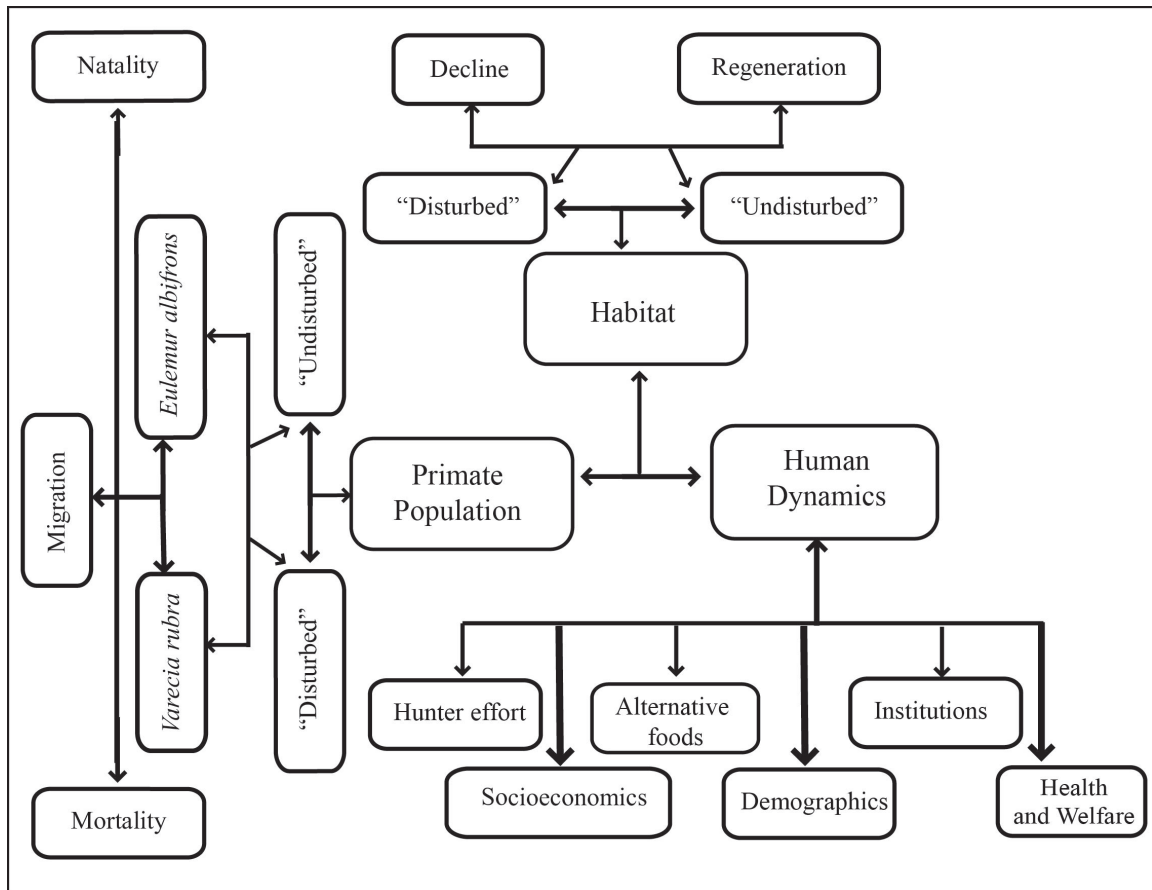


Figure 10. Conceptual model of primate, habitat, and human interactions on the Masoala Peninsula of Madagascar (2011-2012).

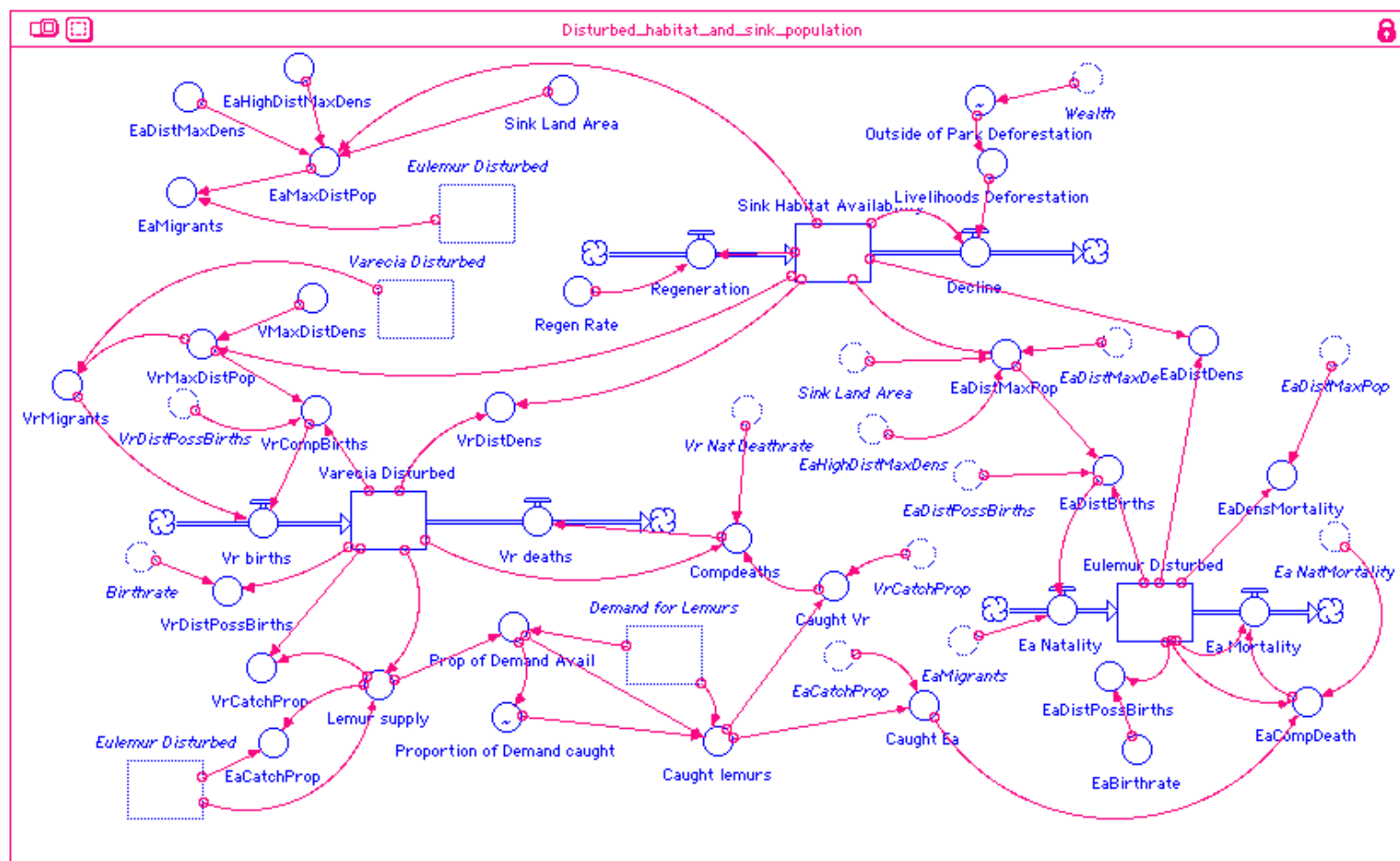


Figure 11. Simplified empirical model of the "disturbed" habitat subsystem including habitat and two species of endangered lemur at a focal site on the Masoala Peninsula of Madagascar (2011-2012).

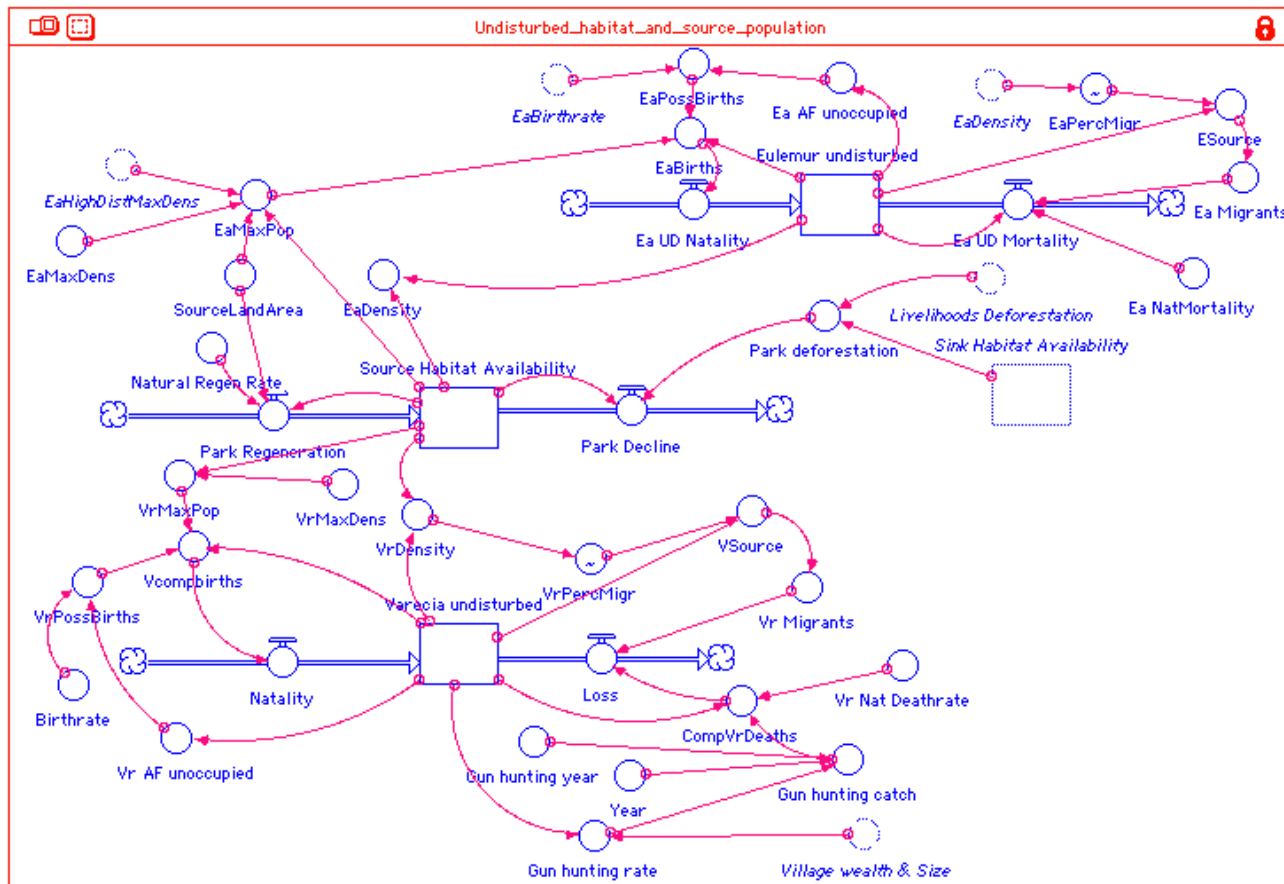


Figure 12. Simplified empirical model of the "undisturbed" habitat subsystem including habitat and two species of endangered lemur at a focal site on the Masoala Peninsula of Madagascar (2011-2012).



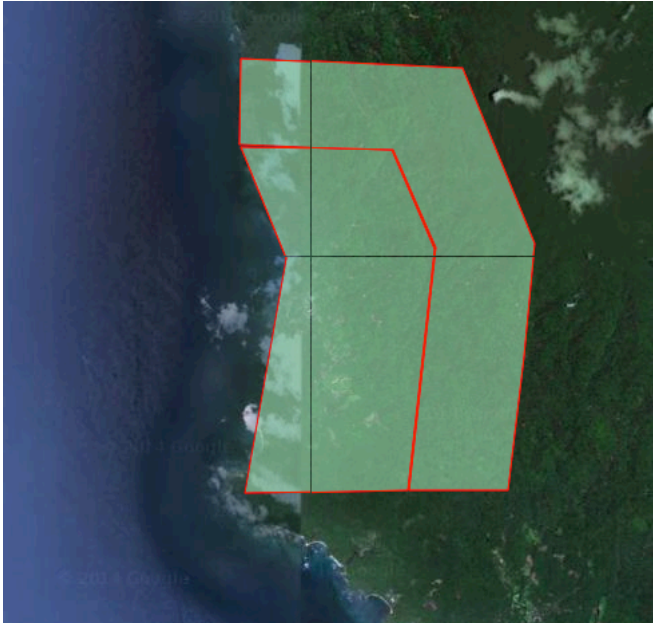


Figure 14. The "disturbed" and "undisturbed" habitat systems within the model.

### **Empirical Model**

The empirical model was represented mathematically as a discrete-time, deterministic model based on different equations with a 1-year time-step. Simulations were run using STELLA 10.0 (isee systems 2014). The empirical model was comprised of three subsystems: an "undisturbed" source habitat and lemur subsystem; a "disturbed" sink habitat and lemur subsystem; and a human village subsystem (Figures 11-13).

### **Habitat**

Habitat ( $H_t$ ) was represented as the total  $\text{km}^2$  of available forest habitat within both the "undisturbed" ( $UH_t$ ) and "disturbed" ( $DH_t$ ) subsystems (1). We defined the "undisturbed" habitat subsystem as a  $10 \text{ km}^2$  area surrounding the village (Figure 14). This area was determined using data on lemur trapping, which occurred within 2,000 meters from the village into the forest interior and 5,000 meters from the village along

the coast (the coast is less steep and therefore people can travel a longer distance and still return home for lunch). We defined the “undisturbed” habitat subsystem as a 10 km<sup>2</sup> area of forest protected within the national park and contiguous with the “disturbed” habitat subsystem (Figure 14). We determined the habitat availability and quality in these subsystems using 30 20m diameter forest plots (Chapter 2).

Temporal dynamics of the state variables representing available forest habitat ( $\dot{H}_t$ ) are calculated as functions of natural regeneration ( $R$ ) and deforestation ( $DD$  and  $UD$ ):

$$\dot{H}_t = (DH_t \cdot R - DH_t \cdot DD) + (UH_t \cdot R - UH_t \cdot \left( \text{if } DH_t > 0 \text{ then } UD \text{ else } UD + \frac{DD}{2} \right)) \quad (1)$$

Deforestation within the “disturbed” habitat ( $DD$ ) was modeled at a rate of 6.7% per year based on data collected during the study year (2 of the 30 habitat plots were converted to farmland).  $DD$  was also modeled as a log function of wealth; the wealthiest households in the village cleared the greatest amount of land. Deforestation within the “undisturbed” habitat ( $UD$ ) was modeled at an initial rate of 1.27% per year (Allnutt et al. 2014). After all of the “disturbed” habitat is converted for agricultural use, deforestation increases within the “undisturbed” habitat, albeit at a lower rate (1).

### **Lemurs**

We determined the density of both lemur species using distance sampling methods in 20 triangular transects, 10 in each of the habitat subsystems. Temporal

dynamics of state variables representing *Varecia rubra* ( $Vr_t$ ) and *Eulemur albifrons* ( $Ea_t$ ) were calculated as functions of the natality ( $VB$ ), natural mortality ( $NM$ ), migration ( $Mi$ ), and hunting ( $Hv$  and  $He$ ) within the “disturbed” ( $D$ ) and “undisturbed” ( $U$ ) subsystems:

$$\dot{Vr}_t = ((DVB + VMi) - (NM + Hv)) + ((UVB) - (NM + Hv + VMi)) \quad (2)$$

$$\dot{Ea}_t = ((DEB + EMi) - (NM + He)) + ((UEB) - (UEM + EMi)) \quad (3)$$

The population size of each of the two lemurs was calculated from densities determined from lemur survey data at the “disturbed” site (6.17 *V. rubra* and 6.5 *E. albifrons* per km<sup>2</sup>) and nearby the “undisturbed” site (16.58 *V. rubra* and 49.84 *E. albifrons* per km<sup>2</sup>) (Chapter 2). Assuming a maximum *Varecia rubra* community home range size of 58 hectares and a *Eulemur albifrons* home range size of 13 hectares (Vasey 2000), these two subsystems could sustain a maximum of 34 *V. rubra* and 154 *E. albifrons* communities.

The birth and migration rates of both lemur species were modeled as density dependent. The birthrates for *V. rubra* and *E. albifrons* were modeled as 0.43 and 0.45 births per adult female per year respectively (Rakotondratsima & Kremen 2001). We modeled the mortality rates in each species as a function of natural mortality and deaths from hunting. The sensitivity of each lemur species to alteration of habitat and hunting was modeled using data from Chapter 2.

The number of *V. rubra* trapped ( $T\dot{Vr}_t$ ) in the “disturbed” habitat subsystem was modeled as a function of their proportion of total lemur supply ( $\frac{Vr_t}{Ea_t + Vr_t}$ ), how easy they



are to catch relative to *E. albifrons*  $\left(\frac{V\dot{r}_t}{E\dot{a}_t + V\dot{r}_t}\right)$ , the demand for lemurs by the local community ( $DemL$ ), the proportion of that demand that can be met by the total lemur supply  $\left(\frac{DemL}{E\dot{a}_t + V\dot{r}_t}\right)$ , and the proportion of those lemurs that were actually caught ( $PrLC$ ):

$$T\dot{V}r_t = \left[ \left[ \left( \frac{V\dot{r}_t}{E\dot{a}_t + V\dot{r}_t} \right) - \left( \frac{V\dot{r}_t}{E\dot{a}_t + V\dot{r}_t} \right) \right] \cdot \left[ \left( PrLC \cdot \left( \frac{DemL}{E\dot{a}_t + V\dot{r}_t} \right) \right) \cdot DemL \right] \right]_{dt} \quad (4)$$

A similar formula was used to model the number of *E. albifrons* caught.  $PrLC$  was modeled as a graphical function dependent on hunter effort and the density of lemurs.

While local people did not trap lemurs in the “undisturbed” habitat (which is protected within the Masoala National Park), gun hunters from other villages have hunted *V. rubra* at the “undisturbed” site within the last ten years. Because of this we also modeled infrequent episodes of gun hunting within the mortality of *V. rubra* in the “undisturbed” site (2).

### Human village subsystem

We modeled our human village subsystem using data on a single village with 118 permanent residents. The human village subsystem represents the demand for lemurs by the local village ( $DemL_t$ ).

$$DemL_t = \left[ \sum_s (W^s X^s) \right]_{dt} \quad (5)$$

### **Net increase in the demand for lemurs**

Net increase in the demand for lemurs was a weighted function ( $W^S$ ) of poverty, child malnutrition, adult morbidity, and human-wildlife conflict driven hunting ( $X^S$ ) (5). These factors and their relative weights were determined using multiple linear regressions of the effect of various human factors on a man's decision to hunt lemurs (Chapter 4).

Poverty was modeled as an inverse function of wealth, which was modeled as a weighted function of base income, salaried work (the dependability of cash income), and illegal export of forest and marine products. The majority of emigrants to the area are attracted by the economic opportunities provided by the illegal extraction of precious woods and sea cucumbers. Illegal export was modeled as a function of illegal logging and illegal sea cucumber collection, and illegal logging. Illegal collection of sea cucumbers was functions of population growth and compliance with collection and export laws. Baseline levels for the compliance with collection and export laws were based on the percentage of village households that comply with forestry laws (had not harvested rosewood (*andramena*) or melicop (*bilahy*) (4 out of 36 households, or 11%).

The child malnutrition scale is a ranked function of the total percentages of children in the village who are: (1) stunted, (2) wasted, and (3) have severely low BMI (max of 300%). To determine this scale, I first calculated the total percentage of children that were more than 2 standard deviations from the standard centiles in height, weight, and BMI (WHO 2006; CDC 2000) (which categorizes them as stunted, underweight, and of severely low BMI respectively). Within the village 43% of all

children were stunted, 54% were underweight, and 22% had severely low BMI for their age (a total of 119%). The prevalence of children who were stunted, underweight, or had severely low BMI for their age was higher in households that trapped lemurs than in those that did not (86%, 71%, and 29% vs. 49%, 39%, and 21% respectively) (Chapter 4). Child malnutrition was modeled using an inverse log function of health based on collected data ( $\text{Log (Child Malnutrition)} = 5.53 - 1.11 * \text{Health}$ ). Health is a ranked (0-5) weighted function of fish consumption, livestock consumption, lemur consumption, access to treatment, and disease. These factors were selected using multiple linear regressions of the effect of various human factors on adult morbidity and child health (Chapter 4). They were weighted based on their impact on the number of days an individual was sick in the last month, and on their age-adjusted height, weight, and BMI (Chapter 4).

Adult morbidity is a ranked function of the number of days in the prior month an adult man was ill. Baseline adult morbidity was set at 4.2 ( $\leq 10$  days). This was determined from data which revealed that lemur hunters were sick an average of 12 days in the prior month, whereas men who did not hunt lemurs were sick an average of 6. Adult morbidity was also modeled as a linear function of health.

We modeled human-wildlife conflict (HWC) driven hunting as a linear function of HWC using a regression of HWC species that stole food on the species that were then hunted because they stole food (significant  $P < 0.0001$ ). The mean number of species hunted due to HWC in each household was 1.4. Human wildlife conflicts (HWC) is a ranked scale of the mean number of animal species that stole food (typically crops or

domestic livestock) from a household. Values were calculated from the range in the village data and the baseline data was set at 3.2. To model the relationship between HWC and livestock ownership, we also made HWC a function of livestock ownership.

### **Net decrease in demand**

We modeled the net decrease in demand as a weighted function ( $W^S$ ) of compliance with hunter effort, hunting laws, salaried work, ecotourism, education, fish consumption, and livestock consumption ( $X^S$ ) (5). Hunter effort was modeled as function of the proportion of the demand met by the supply of lemurs.

Compliance with hunting laws, salaried work, ecotourism, and knowledge of laws were ranked (0-5) using the percentage of village households that comply with hunting laws. Four of 36 household complied with hunting laws (11%). Compliance with hunting laws was also modeled as a weighted function of knowledge of laws and enforcement of laws. All of the villagers knew that hunting was illegal, but the enforcement of hunting laws was low. Forty-six percent of households had a member with a salaried job and 50% had a member who had worked in ecotourism. Education was ranked using the mean number of years members of a household had attended school (village mean = 3.4). Fish and livestock consumption were modeled as the average number of meals per day that contained that animal food over one year (max 3; village average for fish = 1.15, domestic livestock = 0.09). The consumption of fish and domestic livestock were also modeled as functions of wealth and the availability and cost of these animals.

## **Results**

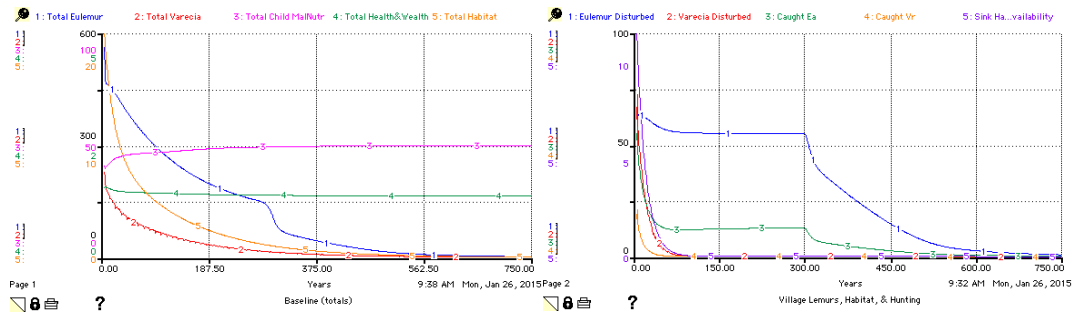
### **Baseline**

Under current conditions at our study site, *Eulemur albifrons* and *Varecia rubra* will be completely extirpated from the site within 854 and 557 years respectively (Figure 15.A). There will be fewer than 10 individuals of each of these species (with an effective population size lower than 4) within 540 and 350 years respectively. Wealth and health will decrease and child malnutrition will increase in the village; over 50% of children will be stunted, wasted, and have severely low body mass indices (BMI). There will be no remaining forest cover within 391 years.

Within the “disturbed” habitat and lemur subsystem, *E. albifrons* will be extirpated within 673 years with a population size of less than 10 individuals in 487 years. The number of *E. albifrons* caught each year will decrease to 12-13 in 55 years and remain at that number for nearly 250 years (Figure 15.B). The last *E. albifrons* will be caught in 619 years. *V. rubra* will be extirpated in 79 years, with a population size of less than 10 individuals in merely 32 years. The number of *V. rubra* caught will rapidly decrease to 0 per year over the next 43 years. As the lemur population decreases, the effort required by hunters to catch them increases, and the demand for lemurs decreases (Figure 15.C). All forest habitat will be converted to agricultural use (including fallow land) within 51 years (Figure 15.B).

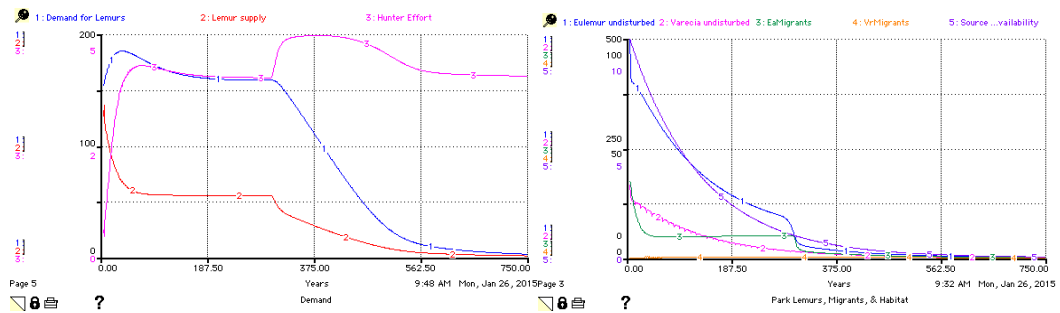
Within the “undisturbed” habitat and lemur subsystem, *E. albifrons* steadily decreases to 30% of its original size over the next 284 years, at which point mortality rapidly increases. *E. albifrons* will be extirpated from this subsystem in 829 years, with

a populations of less than 10 individuals in 446 years. On average, 35 *E. albifrons* will emigrate from this habitat to the “disturbed” habitat to replace lemurs caught by trappers each year during the first 34 years. Migration decreases to 10 individuals per year as the population rapidly declines (Figure 15.D). *V. rubra* will be extirpated from this area in 557 years, with a population size of less than 10 individuals in 354 years. Because of the strict niche requirements of *V. rubra*, and the rapid decline of habitat at the “disturbed” site, no more than one individual emigrates per year and no lemurs emigrate after 55 years. All forest habitat within the park at this site will be lost within 393 years.



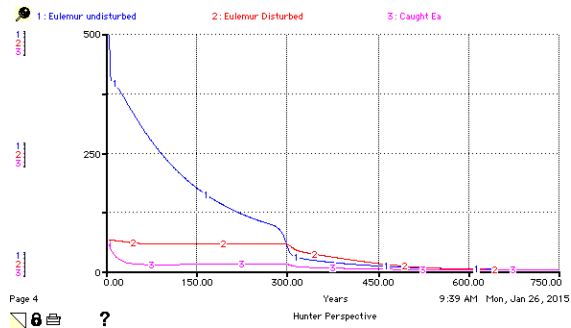
A.

B.



C.

D.



E.

Figure 15. Baseline results of a discrete-time, deterministic, model of a lemur, habitat, and human system on the Masoala Peninsula of Madagascar.

Simulations were run using a 1 year time-step using STELLA 10.0.

Although the total *E. albifrons* population drops to less than 17% of its original size over 300 years, the population at the “disturbed” site remained constant during this time (Figure 15.E). Because of this, hunters are unlikely to be aware of the crash in the *Eulemur* population; the rapid decline in total population did not affect the number of *E. albifrons* caught (Figure 15.E) or the demand for lemurs (Figure 15.D) over this time.

### Scenarios

We tested the effects of various hypothetical scenarios on *Eulemur albifrons*, *Varecia rubra*, forest habitat, and human health and wealth (Table 14). In order to evaluate the sustainability of hunting, we modeled a hypothetical scenario without habitat loss to isolate the effect of hunting on the persistence of the lemur communities. Once the effects of habitat loss were eliminated, the hunting of both lemur species was sustainable (Table 14). Under the assumption that the source and sink habitat regions are of equal size (in this case, 10 km<sup>2</sup>), migration from the “undisturbed” population supported the “disturbed” population in a stable source-sink dynamic.

Only after we modeled a hypothetical scenario where we: (1) reduced corruption and increased law enforcement; (2) developed opportunities for viable economic alternatives; and (3) expanded the rural banking system and made involvement in that banking system a requirement for participating in the economic development activities, were we able to secure the future viability of lemurs, habitat within and outside of the park, and the health and welfare of local people (Table 14). The loss of habitat within the “undisturbed” habitat can be slowed by reducing corruption within the National



Park system and by increasing law enforcement. However, when this intervention was applied alone, it increased poverty and child malnutrition within the village (Table 14). Therefore this policy, alone, is unacceptable; not only would it be inhumane, but it would damage the relationship between the park and local people and increase the incentives for the illegal behavior it was meant to stem (Chapter 4). To mediate the negative effects of law enforcement on local people, we included alternative economic development (AED). Poverty was found to have the greatest impact on human health. By increasing rural wealth, this scenario reduced the incentives for illegal hunting and offset the negative effects of reducing habitat loss through increased enforcement; however AED also increased habitat loss outside of the park, which increased the incentive to clear land within the park once this land is 'lost'. Habitat loss at the site was positively correlated with wealth. Once an individual increases his wealth, he or she reinvests that wealth by clearing more land for agriculture. Because there are no local banks, there are few secure alternatives for investing in one's future.

### **Timing**

We built the model using data collected in 2011-2012. We modeled the scenarios above assuming all interventions were applied immediately and simultaneously three years ago (they were not). When a conservation scenario is implemented may affect conservation outcomes. Using the most effective conservation scenario above (a three pronged plan of alternative economic development, reduce corruption and increase law enforcement, and the development of rural banks), we tested the effects of different timing during a 10-year conservation plan on conservation

outcomes over 100 years (Table 15). Because three years have passed since the data for the baseline of this model, the earliest conservation actions were implemented at year 4. Considering: (1) limited manpower and funds; and (2) the challenge of reaching the villages surrounding the park, we allowed two years for the implementation of each of the three conservation strategies. We also tested a simultaneous plan at year 6, which was modeled with a delayed start time because of the extra time needed to develop and implement all three approaches simultaneously (Table 15).

Table 14. Effects of scenarios on the persistence of *Eulemur albifrons* and *Varecia rubra* populations and available forest habitat, and on the health, wealth, and percentage of malnourished children in a village at a site on the Masoala Peninsula.

Scenario <sup>a</sup>	<i>E. albifrons</i> <sup>b</sup>	<i>V. rubra</i> <sup>b</sup>	Habitat <sup>c</sup>	Human health & wealth <sup>d</sup>	Prevalence of stunted and wasted children <sup>e</sup>
Baseline	854/540	557/350	390	1	50%
No hunting	>1000	734/352	390	1	67%
No habitat loss	>1000	>1000	>1000	1	63%
Reduce corruption and increase law enforcement (C&L)	>1000	>1000	>1000	1	45%
Alternative economic development (AED)	855/494	550/350	390	3	7%
Development of rural banks (B)	857/545	624/401	481	1	50%
Improve poultry production (P)	862/548	558/350	390	1	50%
Increase ecotourism and education	854/540	557/350	390	1	50%
AED and B	852/475	750/373	481	3	7%
<b>AED, B, and C&amp;L</b>	<b>&gt;1000</b>	<b>&gt;1000</b>	<b>&gt;1000</b>	<b>3</b>	<b>7%</b>
P and C&L	>1000	>1000	>1000	1	45%

<sup>a</sup> We have bolded the most preferred scenario

<sup>b</sup> Years until complete extirpation (a population size of 0)/Years until a population reduction to less than 10 individuals (a group with an effective population size lower than 4)

<sup>c</sup> Years until 0 natural forest cover

<sup>d</sup> Ranked from 0 (low) – 5 (high). Calculated from the mean scores of adult morbidity, child health and growth, and wealth (as determined from the size and construction of houses)

<sup>e</sup> Percentage of the total population. Calculated as the mean of three percentages (stunting, wasting, and severely low BMI)

Table 15. Examples of the effect of timing on conservation outcomes over 100 years at a focal site on the Masoala Peninsula, Madagascar.

Conservation outcomes after 100 years								
Year implemented <sup>g</sup>	C&L <sup>a</sup>	AED <sup>b</sup>	B <sup>c</sup>	Habitat (Park low)	<i>Varecia</i> <sup>d</sup> (Park)	<i>Eulemur</i> <sup>d</sup> (Park)	Human health and wealth <sup>e</sup> (Low)	Child Malnutrition <sup>f</sup> (Low)
	4	6	8	13.1 km <sup>2</sup> (9.7)	161 (138)	482 (425)	3 (1)	6% (70%)
	4	8	6	13.4 km <sup>2</sup> (9.7)	159 (138)	481 (424)	3 (1)	6% (70%)
	6	4	8	12.7 km <sup>2</sup> (9.5)	156 (139)	481 (425)	3 (2)	6% (40%)
	8	6	4	13.7 km <sup>2</sup> (9.4)	162 (138)	481 (423)	3 (2)	6% (40%)
	<b>6</b>	<b>6</b>	<b>6</b>	<b>13.4 km<sup>2</sup> (9.5)</b>	<b>160 (138)</b>	<b>482 (424)</b>	<b>3 (2)</b>	<b>6% (40%)</b>

<sup>a</sup> Reduce corruption and increase law enforcement

<sup>b</sup> Alternative economic development

<sup>c</sup> Establishment of rural banks

<sup>d</sup> Population size (n)

<sup>e</sup> Ranked from 0 (low) – 5 (high). Calculated from the mean scores of adult morbidity, child health and growth, and wealth (as determined from the size and construction of houses)

<sup>f</sup> Percentage of the total population. Calculated as the mean of three percentages (stunting, wasting, and severely low BMI)

<sup>g</sup> We have bolded the most preferred scenario

The most preferred scenario was the plan where all three interventions were applied simultaneously during year 6. If we applied the results of this scenario to the entire peninsula, we would be able to save an additional 4% of “undisturbed” habitat within the park, 3% of the population of *E. albifrons* and 14% of *V. rubra* outside of the park, and 85.6 km<sup>2</sup> of “disturbed” habitat outside of the park. We would also reduce the prevalence of malnutrition to 6% of children while preventing an initial increase to 70%.

These gains were achieved solely by determining the most effective time to implement these plans. Two scenarios were more effective at reducing habitat loss; had we selected these we would have saved an additional 32.1 km<sup>2</sup> of habitat. However we rejected these strategies because early during the simulation they increased the prevalence of child malnutrition and poor growth to 70% of all children.

### **Discussion**

While our understanding of the linear effects of habitat and hunting on endangered lemurs is improving (Chapter 2), we have little information on how the dynamic interactions of humans, endangered lemurs, and habitat. We applied a system dynamics approach to understand the long-term persistence of lemurs and habitat, and the health and welfare of people at a single site on the Masoala Peninsula. Unless circumstances change, our simulations suggest that we will lose two species of lemur, two forest habitats, and the security of the health and welfare of the local people. The annual rate of deforestation and disturbance outside of the park was 6.7% at our site, more than seven times the national average (Harper et al. 2008) and five times the rate within the Masoala National Park (Allnutt et al. 2013).

In spite of this, the circumstances for lemurs are more hopeful at our site than they may be elsewhere on the Masoala. The population size of *Eulemur albifrons* is suspected to have decreased by over 50% in the last 24 years and the population size of *Varecia rubra* is expected to decrease by more than 80% over the next 24 years (IUCN 2014). Our simulations suggest that the reduction of *E. albifrons* and *V. rubra* at our site will slow over the next 24 years to 24% and 42% respectively.

However, our model assumes a source population of lemurs in an area of “undisturbed” habitat that is equal in size to the “disturbed” area surrounding a small village. These assumptions cannot be met throughout the entire peninsula. The Masoala National Park protects 2,140 km<sup>2</sup> of habitat (Kremen et al. 1998). The area surrounding the park has 250 permanent villages with a total population of more than 85,000 people in 2007 (Holmes, 2007). This allows for an average of 8.56 km<sup>2</sup> of park per village, or 2.5 ha<sup>2</sup> per person. Our model allowed 10 km of park for the village, or 8.5 ha per person. If we adjust our source population to the average allowance per person on the peninsula (a source area of 2.95 km<sup>2</sup>), the population of *E. albifrons* decreases by 44%, and *V. rubra* by 59%. There is also a forested buffer zone between the park and our study village that is large enough to prevent subsistence snare trapping within the park; other villages do not have similar buffer areas.

Conservationists and public health officials face serious challenges in implementing their action plans on the Masoala Peninsula. Corruption on the peninsula is high, and conservation efforts are unlikely to match the economic “incentives” offered by those who illegally export precious woods (Waeber and Wilmé 2013) and sea cucumbers (Borgerson unpublished data). There are shrinking forest corridors in the NW of the peninsula as little as 200 meters across which threaten to isolate lemur populations there (PN Masoala 1999). The large park has 1 kilometer of park boundary for every 4.37 km<sup>2</sup> of park, is extremely rugged, contains no roads, is typically covered in cloud cover, and has rough seas most of the year down its eastern coast. This makes the practicalities of conservation efforts and monitoring challenging. The park also has a

limited budget and is unable to enforce the laws it creates (jurisdiction of the national military police) or to regulate the severity of corporal punishment on law-breakers. Finally it has poor relations with many of the local people (Ormsby & Kaplan 2005, Keller 2008). Given these challenges, it is important to isolate cost effective targeted solutions to conservation and public health challenges.

The social variables most critical in influencing local lemur population viability are poverty/wealth, corruption and law enforcement. Poverty and wealth had complex effects on lemur populations; poverty increased hunting and reduced human health, and wealth increased forest clearing. We identified a three pronged approach to secure the future viability of lemurs, habitat within and outside of the park, and the health and welfare of local people: (1) reduce corruption and increase law enforcement; (2) develop opportunities for viable economic alternatives; and (3) expand the rural banking system and make involvement in that banking system a requirement for participating in the economic development activities. This plan is most effective when its components are implemented simultaneously during year 6. However, the success of this simulation may be deceptive, as the plan requires the success of three separate sub-components. Because wealth indirectly improves child health and adult morbidity, more research is needed to identify the factors that most directly influence child health. If we can directly increase child health and reduce adult morbidity, we may be able to decrease wealth-driven habitat loss. This would allow us more time, after addressing the root causes of system behavior, to establish a rural banking system.

We tested a scenario where we increased the production of poultry to more directly influence human health, but this scenario neither improved human health nor the persistence of lemur populations. More research must be done to isolate the root causes of poor child health on the peninsula; possibilities include variation in food security and access to carbohydrates, fats, and micronutrients.

To understand the future population viability of *V. rubra* and *E. albifrons* and to better isolate how human factors affect (and are affected by) habitat, lemurs, and human health, we recommend that future research: (1) survey many diverse villages surrounding the park, and (2) further examine the correlates of child malnutrition and poor growth and the impacts of wealth on habitat loss. We also recommend that habitat and lemurs be surveyed within the interior of the peninsula to further assess the stability of peninsula-wide source-sink dynamics. Expanding this systems approach on the Masoala Peninsula will help ensure that we are not only able to diagnose current problems in primate conservation, but also able to uncover the ultimate drivers of primate system behavior, substantially enhancing the attainability of lemur conservation while improving human health and welfare.

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## CHAPTER 6

### CONCLUSIONS

Although, humans and ecosystems are intimately related, surprisingly few scientists have quantitatively investigated how they affect each other, or what role human incentives play in driving this interaction. This dissertation examined the dynamic interactions among human health and welfare, illegal resource use, and forest ecology in one of the most biodiverse places on earth, the Masoala Peninsula of Madagascar (Kremen et al. 1998, Holmes 2007, Kremen et al. 2008). I addressed the following four questions with the goal of increasing the attainability of conservation goals on the Masoala Peninsula:

#### **(1) Should we even focus our conservation efforts on hunting?**

Yes, but specific conservation policies must be designed with their differential impacts on lemur species in mind. Alteration of habitat and hunting shapes local faunal communities in species-specific ways. While alteration of habitat has a greater effect than snare trapping on the populations of *Varecia rubra*, snare trapping has a greater effect than habitat on the populations of *Eulemur albifrons*. Therefore conservation action plans for *V. rubra* and *E. albifrons* may benefit from individual tailoring. Both will depend on working with local people to develop viable options that increase the sustainability of their livelihoods. *V. rubra* may benefit from a greater emphasis on reducing alteration of habitat, especially the loss of large trees with voluminous crowns. *E. albifrons* may instead



benefit from a greater emphasis on increasing the sustainability of human food systems. Chapter 2 illustrates the need to consider the different manners in which habitat change and hunting affect sympatric primate species when designing conservation policy.

**(2) When do people hunt lemurs, and how can this help us to optimize conservation efforts?**

There is strong seasonal variation in the hunting of forest mammals and the consumption of fish and domesticated livestock. Hunters target bushpigs, tenrecs, and endangered lemurs during the cool, wet austral winter (March – August). In contrast, people eat more threatened euplerid carnivorans (e.g. *Cryptoprocta*, *Fossa*), introduced viverrids, fish, and domesticated livestock during the warm austral summer (September – February). Euplerid and tenrec hunting coincided with these animals' pregnancy and lactation, increasing the impact of hunting on these species. Seasonal increases in hunting also coincided with food insecurity within the human community. However, seasonal changes in hunting patterns were driven by the physical and behavioral characteristics of prey rather than seasonal scarcity of animal-based foods. Chapter 3 illustrates an important aspect of hunting on the Masoala: the incentives for hunting in general are not the same as the incentives for seasonal patterns in hunting. Conservationists may be most effective on the Masoala if they design their policies to address the overall incentives for hunting, and time their individual species-specific action plans to coincide with either the hunting of endangered euplerids during the austral summer, or the hunting of tenrecs and endangered lemurs during the austral

winter. Similarly efforts to improve the health and welfare of local people may be more effective if they are timed to coincide with the reduced availability of alternative animal-based foods during the austral winter.

### **(3) Who hunts lemurs and why?**

Of numerous potential reasons (including demographics, human health, livestock ownership, wealth, education, knowledge of laws, involvement in ecotourism, and other cultural factors) an individual's sex, health, and wealth most accurately predicted a person's decision to engage in illegal lemur trapping. Notably, neither working in ecotourism nor knowledge of hunting laws had an impact on the decision to trap lemurs. These findings support growing evidence that the key to successful lemur conservation may be improving rural human health and welfare. Solidarity among hunters, researchers, policy makers, and implementers throughout conservation and public health action is essential. Because of the strong relationship between a man's decision to illegally trap lemurs and his wealth, health, and the health of the children in his household, I recommend that conservation and human health initiatives combine their efforts and make improving rural welfare and child health a central component of lemur conservation on the Masoala Peninsula.

**(4) How do the dynamic interactions of lemurs, habitat, and humans, impact their respective futures? How can we use this information to improve the efficacy of conservation and to design conservation strategies that are mutually beneficial for wildlife and human health and welfare?**

I applied a system dynamics approach to understand the long-term persistence of lemurs and habitat, and the health and welfare of people at a single site on the Masoala Peninsula. Unless circumstances change, our simulations suggest that we will lose two species of lemur, two forest habitats, and the security of the health and welfare of the local people. The annual rate of deforestation and disturbance outside of the park was 6.7% at our site, more than seven times the national average (Harper et al. 2008) and five times the rate within the Masoala National Park (Allnutt et al. 2013). We identified a three-pronged approach to secure the future viability of lemurs, habitat within and outside of the park, and the health and welfare of local people. However, the success of this simulation may be deceptive, as the plan requires the success of three separate sub-components. To understand the future population viability of *V. rubra* and *E. albifrons* and to better isolate how human factors affect (and are affected by) habitat, lemurs, and human health, we recommend that future research: (1) survey many diverse villages surrounding the park, and (2) further examine the correlates of child malnutrition and poor growth and the impacts of wealth on habitat loss. We also recommend that habitat and lemurs be surveyed within the interior of the peninsula to further assess the stability of peninsula-wide source-sink dynamics. Expanding this

systems approach on the Masoala Peninsula will help ensure that we are not only able to diagnose current problems in primate conservation, but also able to uncover the ultimate drivers of primate system behavior, substantially enhancing the attainability of lemur conservation while improving human health and welfare.

### **What next?**

Effective conservation depends on innovation, transparency, incredibly hard work, and a rich substantive understanding of ecology and the choices humans make within their dynamic social and ecological system contexts. I am working towards securing both the livelihoods of local people and the future integrity of threatened species and ecosystems. Over 24 months (June 2015 – May 2017) I will expand my research to address the needs identified within this dissertation. Specifically, at 14 diverse sites surrounding the Masoala National Park, I will: interview members of over 400 households; measure the health of over 2,000 individuals; monitor the daily behavior of 5 focal illegal endangered species hunters; monitor forest ecology at 140 habitat plots; survey two endangered lemur species in 140 regional transects and across a trans-peninsula transect of over 110 aerial kilometers; build a system dynamics model of human-forest-endangered lemur interactions; design an integrated human-health and conservation action plan, and implement this plan in 7 ‘test’ communities. It is my goal to directly improve child health and the future of endangered species in one of the most threatened and food insecure habitats on earth. Additionally, this future research will (1) inform the decision making of conservation and public health policy-makers through

an active engagement with diverse stakeholders that range from hunters, to the director of the Masoala National Park, and public health and conservation NGOs; and (2) translate these interdisciplinary scientific findings into applied integrated conservation and public health action on the Masoala, while simultaneously monitoring conservation targets (i.e. critically endangered lemur species, forest ecology, and human health) to identify rebounds in lemur population size, changes in hunting behavior, and their impact on local people's health, economy, and well-being. Success will be difficult, but if we can do this on the Masoala Peninsula, one of the most threatened ecosystems and poorest places on earth, we can adapt this approach to improve the outcomes of conservation and public health actions worldwide.

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